

CONSERVING FORESTS: A BIOPHILOSOPHICAL ANALYSIS
OF THE DURBAN REGION

by

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PREFACE

The work described in this thesis was carried out in the Department of Biology, University of Natal, Durban from January 1990 to June 1992 and from July to December 1993 under the supervision of Professor J.C. Poynton.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

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ABSTRACT

Coastal forests are a significant component of the remaining natural vegetation in the greater Durban area. Being closely associated with an historical and rapidly developing urban environment, these forests are invariably small, isolated and variously disturbed. The nature of disturbance as an ecological phenomenon, coupled with unknowable disturbance histories and ongoing disturbance events poses particular challenges to traditional and tradition-bound attempts to understand and manage such forests.

The intention of this study was to discuss as deeply as possible the nature of such challenges, while at the same time considering the broader relevance of practising ecology in the urban environment.

At a practical level the forests were sampled in an attempt to describe forest communities, to assess the effects of disturbance on them, and to gain insight into the effects of different disturbance histories and regimes on forest physiognomy and floristics with a view to proposing management guidelines. Various descriptive approaches, as well as a multivariate analysis using Detrended Correspondence Analysis were used in an attempt to interpret the data collected.

The unsatisfying nature of the data led the thesis to propose a review of the paradigm in which its methods were rooted. Both the data, and the broader issues on which the thesis touched were discussed in terms of biology's rootedness in philosophical assumptions. This led the thesis to a methodological position aligning it both epistemologically and ontologically with a philosophical method of investigation called phenomenology. While other philosophical contentions were touched upon, the main conclusion of the thesis was that phenomenological thinking, while challenging to apply, was relevant to philosophically mature and methodologically appropriate attempts to conserve the forests with which the thesis was concerned.

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INTRODUCTION

1. Thesis structure and approach

"Everything in life should be made
as simple as possible, but not simpler"

--- Albert Einstein ---

"Science at its highest level is ultimately
the organisation, the systematic pursuit,
and the enjoyment of wonder, awe, and mystery"

--- Maslow ---

This thesis attempts a synthesis of information pertaining to our understanding of forest dynamics and management. The aims of this project are:

1. To consider the relevance of practising ecology in urban environments, in this case the greater Durban area, as well as difficulties and theoretical limitations in doing so. To discuss aspects of the literature that are broadly relevant to conservation practice, in the spirit that part of the nature of solutions is an awareness of the scope and complexity of the problem.
2. To assess the effects of past and present disturbance regimes on community structure and composition for five Durban forests.
3. To generate useful comparisons within and between forests, allowing for quantitative elaboration of the effects of different disturbance histories on forest physiognomy and floristics.
4. To explore the results of the quantitative investigations in an attempt to highlight ideas relevant to the conservation and management of these forests.

Essential to this thesis is the belief that "Biology is rooted in philosophical assumptions" (Sattler, 1986) and that, especially in ecology, no effort should be spared in thinking deeply and clearly about the nature of problems encountered. In the complex field of forest ecology and conservation, the following comment of Sloan (1979) is particularly apposite, and sets the stage for the approach and discussion to come.

"The practising scientist is often so busy gaining and interpreting information in his own particular field of study

that he has little time to consider the broader issues of what science is about and how it should be performed". Poynton (1991) comments that this "not infrequently leads scientists to misunderstand the nature and implications of their own work" and that this leads to "wasted research time and effort". Indeed, Whitehead (1926) states that if science is not to degenerate into a medley of *ad hoc* hypotheses, that it must "become philosophical and must enter upon a thorough criticism of its own foundations" (Whitehead, 1926 in Sloan, 1979). The importance of this perspective is further asserted by Sattler (1986), and Maheu (1965) in Sloan (1979) who states that "The essence of science is not knowledge but the method by which knowledge is gained, the rule the mind prescribes itself in order to attain it".

This epistemological problem requires some philosophical investigation because while "methodology is the basis of science, it is not the whole story" as "Metaphysical principles are involved in most scientific reasoning" (Sloan, 1979; Sattler, 1986).

Whiteman (1986) boldly sums up some consequences of this idea in his statement that: "Most leaders of thought today realise that physics, depth psychology, the mystical in religion, and the phenomenological method in general have shown that 'science' is meaningless or untrue without its non-physical depth".

The importance of Sattler's (1986) contention that "biophilosophical awareness has existential and social dimensions" is also touched upon.

While the constraints of an M.Sc. prevent any really thorough treatment of such philosophical contentions, this thesis attempts at least to acknowledge them wherever it can in the hope that the cumulative outcome of doing so will suggest the enduring importance of philosophical perspectives.

In the interests of accessibility, the thesis has been divided into three parts. Part 1 covers the first eight sections, Part 2 covers sections 9 to 15, and Part 3 includes sections 16 through to the end. Part 1 includes a description of the study area and informs the reader about what work was done, how it was carried out, and what was learnt, both in the process of doing the fieldwork, and in analyzing the data.

Part 2 admits to the unsatisfying nature of the results, and attempts to provide an overview of why the problems encountered exist. This includes a consideration of various theoretical and conceptual problems and perspectives, as well as an overview of the possibilities, problems and challenges inherent in the urban situation.

Part 3 attempts to show that, even when dealing with seemingly routine scientific subjects such as modelling, monitoring, management and the use of established tools such as ordination, the need to reflect deeply on method and approach remains, even if not necessarily always at a philosophical level. Having

introduced the reader to this notion, the thesis concludes with a broad-scale conceptual analysis of the problem of forest conservation in the urban environment, some practical research recommendations, and a philosophical outline of a way forward.

Guidance is given to the reader at appropriate points throughout the thesis, both in calling attention to underlying philosophical problems and perspectives, and in pointing out that existing difficulties and shortcomings in approach and method suggest the need for openmindedness in the consideration of alternative approaches.

The conceptually intricate nature of any biological treatment of the functioning of dynamical non-linear systems places demands on thesis structure and approach. This is reflected in the inclusion of sections which cause the work to appear cumbersome. Given the potential breadth of the topic, no apologies are made for the small print.

2. The study area

Fuggle (1983b) in Roberts, D.C. (1990) states that Durban is the largest city on the east coast of Africa and one of the four largest urban areas in South Africa. Durban is also one of the fastest growing cities in the world (Botha, 1988 in Roberts, D.C., 1990). Durban thus provides a useful arena in which to investigate difficulties that arise when the need for conservation is crucial, but where challenging urban conditions require that a fresh look be taken at tradition-bound scientific procedures.

The area encompassed by Municipal Durban, and in which the study was conducted, is shown in Fig. 1, in which the latitudes and longitudes bounding the Durban area are provided.

The following coastal forests were investigated in the course of this study:

Burman Bush is a 50 ha coastal forest remnant situated approximately 8km north of the Durban C.B.D.. According to Roberts, D.C. (1990) it is both well below the estimated minimum critical area for its community type, as well as being almost completely isolated from areas of similar floristic composition. Roberts, D.C. (1990) predicts that its total ecological isolation, if ongoing, could result in irreparable community degradation.

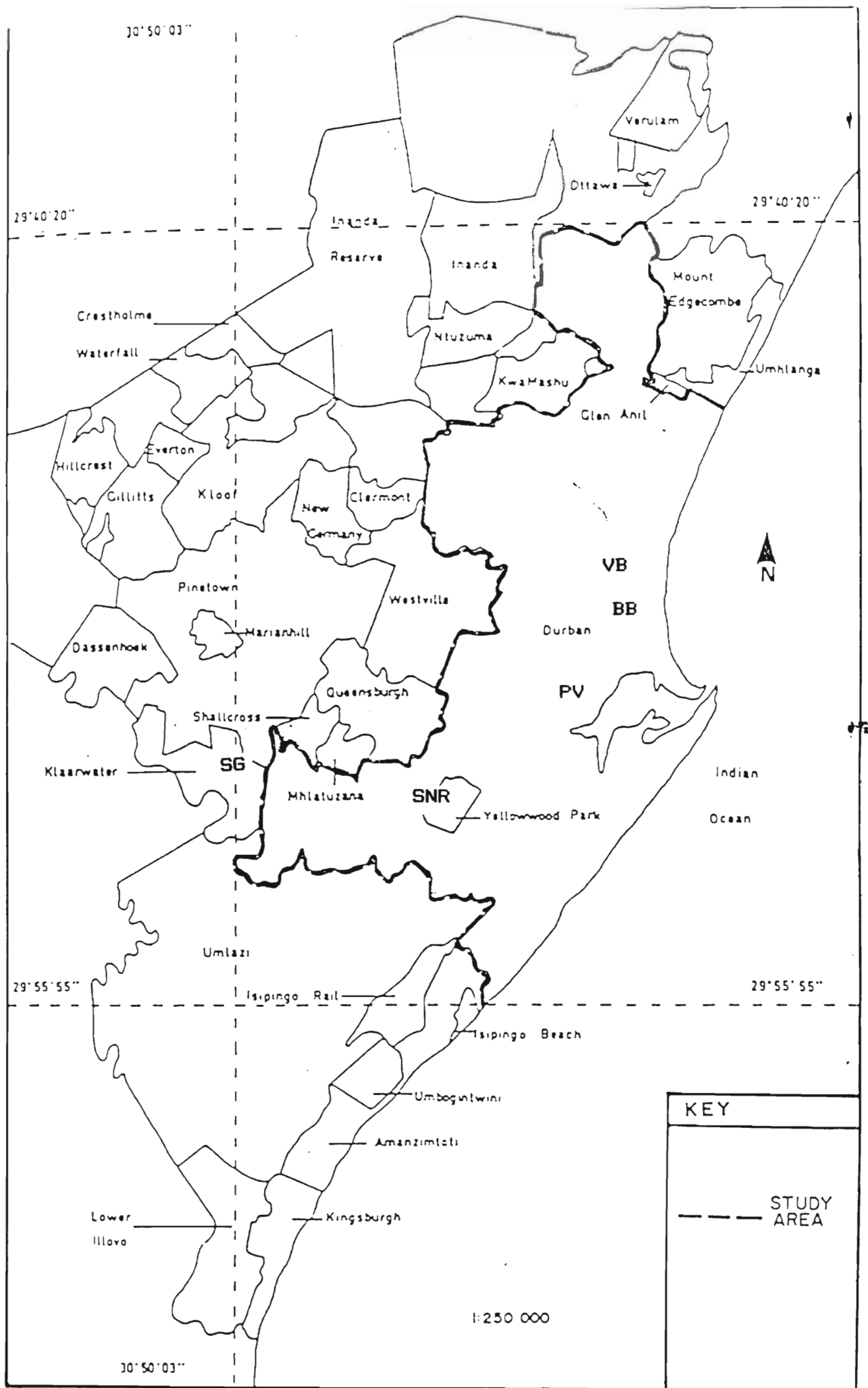


Figure 1. : Map showing the greater Durban area and the position of the five forests with which the study was concerned.

Pigeon Valley is a 10 ha remnant of the once extensive Stella Bush which dominated the east-facing slopes of the Berea ridge, and was initially declared a nature reserve because of the rarity of the Natal Elm, *Celtis mildbraedii*, of which it contains some large specimens. According to Roberts, D.C. (1990), isolation and reduced size have negatively affected Pigeon Valley's prospects for long-term viability, with recruitment of tree species appearing to be limited. The predominance of gaps in the forest strongly supports the notion that in tropical forest systems, areas of 10 ha and smaller are composed entirely of edge (Lovejoy *et al.*, 1986 in Roberts, D.C., 1990).

Virginia Bush, situated approximately 15 km from the Durban C.B.D., is a 38 ha site which originally formed part of the natural coastal bush which joined with the dune bush nearer the coastline. During the late 1800's and early 1900's parts of the area were cultivated by market gardeners. Virginia Bush was also used for military manoeuvres during the Second World War. Although it has had 40 years to recover from these disturbances it has been invaded by many alien plant species.

Silverglen Nature Reserve is a 212 ha forest remnant situated between two rapidly developing community areas. It is a valuable area both in terms of its unique floristic qualities and its combination of forest, grassland and riverine areas. Its size also makes it an important source area for the broader urban landscape (Roberts, D.C., 1990).

Stainbank Nature Reserve. This 214 ha area with its diverse habitats is one of the most important conservation cores within the municipal landscape (Roberts, D.C., 1990). Other than acting as essential species sources and refuge areas, large areas like Stainbank and Silverglen are useful benchmarks against which to assess trends in community dynamics, as they represent the closest approximations to complete landscape units that it is possible to achieve in the urban environment (Roberts, D.C., 1990).

3. Vegetation

The vegetation of Durban falls within the Tongoland-Pondoland Regional Mosaic as defined by White and Moll (1978). This region extends from the mouth of the Limpopo River (25°S) to about Port Elizabeth (34°S) (White and Moll, 1978). In the North this region is about 240 km wide, but in the South where mountains come close to the sea it is locally no more than 8 km wide (White and Moll, 1978). Elsewhere it penetrates along deep river valleys far into the interior (White and Moll, 1978). Of the five main forest types occurring in the Tongoland-Pondoland Regional Mosaic, Sand, Dune, Swamp and Fringing forests occupy specialized sites (White and Moll, 1978). The remaining type is referred to by these authors as 'Undifferentiated lowland forest' and the forests with which this study is concerned are included in this type. White and Moll (1978) describe these forests as being essentially evergreen, with varying proportions of semi-deciduous

species. Forest height and stratification depends largely on local site factors, while canopy heights range from 10 to 30 m (White and Moll, 1978). Canopy trees characteristic of these forests include *Drypetes gerrardii*, *Strychnos* spp., *Vepris undulata*, *Trichilia dregeana*, *Protorhus longifolia*, *Millettia grandis*, *Albizia adianthifolia*, *Brachylaena* spp., *Celtis* spp., *Chrysophyllum viridifolium*, *Chaetacme aristata*, *Ficus* spp., *Croton sylvaticus*, *Combretum kraussii*, *Cassipourea* spp., and *Mimusops obovata*. White and Moll (1978) also note the large number of species of woody lianas associated with disturbance and the extreme difficulty of investigating the ecology of these forests due to the exploitation of all valuable timber trees.

With respect to the sub-canopy layer, these authors note that it is usually well developed, and that this could be partly due to exploitation which has opened up the upper canopy. Common and widespread genera in the subcanopy include *Bequaertiodendron*, *Canthium*, *Clausena*, *Dracaena*, *Drypetes*, *Erythroxylum*, *Eugenia*, *Memecylon*, *Pavetta*, *Peddiea*, *Teclea* and *Tricalysia*, with other fairly common genera being *Allophylus*, *Anastrabe*, *Baphia*, *Buxus*, *Cryptocarya*, *Diospyros*, *Gardenia*, *Ochna*, *Oxyanthus*, *Pancovia*, *Rawsonia*, *Rothmania* and *Xylothea*. The herbaceous layer of this forest is usually well developed with many grasses, sedges and members of the Acanthaceae occurring (White and Moll, 1978).

Natal coastal forests have subsequently been variously described and classified by authors such as Ward (1980), Cooper (1985), Acocks (1988), MacDevette, MacDevette, Gordon and Bartholomew (1989); and by Moll (1976). While such descriptions are of academic interest, they are of little use in characterising the extremely small and highly disturbed forests found in urban areas, where generalised descriptions fail in the face of highly altered vegetation and a range of disturbances at small scales.

4. Climate

The climate of Durban is essentially subtropical, and is moderated strongly by the warm Agulhas current. Temperatures drop as low as 12.2°C in winter, and summer temperatures may be as high as 29°C. The moderating effect of the ocean on temperature extremes is reflected in the fact that the annual range about the mean annual temperature of 20.5°C is only 8.5°C (Preston-Whyte, 1980). Maximum temperatures along the coast may be noticeably higher in September and November during berg wind conditions, but minimum temperatures are not subject to large fluctuations (Preston-Whyte, 1980).

Coastal areas are frost free but inland the deep river valleys may experience light frosts in certain areas (Preston-Whyte, 1980).

Precipitation in the area is experienced mainly as rain which occurs prevalently in summer. 60% of the annual rainfall falls between November and March, and 15% falls between May and August (Preston-Whyte, 1980). The average rainfall is between 1000 mm and 1250 mm per annum (Preston-Whyte, 1980).

5. Geology and soils

While the geological units found within the Durban area are diverse, the geological formations on which the forests under consideration rest occur either on Natal Group Sandstones or on formations that accumulated during the Quaternary Era, including the Bluff Sandstones and the Berea Red Sands (Roberts, D.C., 1990).

The Stainbank and Silverglen Nature Reserves occur on these Natal Group Sandstones, which on breakdown yield a light-grey sandy soil which is often only a few centimetres thick, and of low fertility (King and Maud, 1964 in Roberts, D.C., 1990). Mispah soils are found on upslope positions, Cartref Cartref soils on midslope positions, Kroostad Mkambati soils on lower slope positions and Katspruit Katspruit soils along wet valley lines (Maud pers. comm. in Roberts, D.C., 1990). Characteristics of these soil types are given in Roberts, D.C. (1990).

Sediments of the Quaternary period are associated with the Berea ridge. Burman Bush is situated on an exposure of the Bluff Sandstone Formation while Pigeon Valley and Virginia Bush are found on the Berea Red Sands which overlie Bluff Sandstones on the Berea ridge. Soils characteristic of the Berea Red Sands are the Hutton Clansthal soils, the Hutton Msinga soils and the Fernwood Fernwood soils (Maud pers. comm. in Roberts, D.C., 1990). Characteristics of these soil types are provided in Roberts, D.C. (1990).

6. Materials and methods

For siting of quadrats see section on sampling.

Square 400m² quadrats were used. This size was chosen in accordance with Geldenhuys, Knight, Russell and Jarman eds. (1988) and is accepted as the standardized quadrat size for work within the forest biome (Geldenhuys in Muir, 1990). This size also proved practical, in enabling me to sample relatively homogenous areas of forest reflecting the nature of specific patch types, as well as allowing for the possible comparison of results with those of other biologists working within the forest biome project of the C.S.I.R. (Council for Scientific and Industrial Research). Square quadrats were used because this proved to be the most practical way of overcoming the difficulties of preserving the geometry of quadrats while attempting to lay out such large areas in thick forest.

Four quadrats were placed in Burman Bush (50ha), Stainbank Nature Reserve (214ha), Pigeon Valley (10ha) and Virginia Bush (38ha). Two quadrats were measured in Silverglen Nature Reserve (212 ha) due to time constraints, giving a total of eighteen quadrats. While it is conceded that more quadrats would have contributed to a more accurate picture, time constraints did not allow for any more sampling.

While it would have been advantageous to provide a description of the location of these quadrats such that they could have been relocated, there is no readily available system of geographical referencing that will enable another researcher to relocate quadrats in thick forest. Given the patchy nature of the forests, quadrats would have had to be relocated with 100% accuracy for the exercise of doing so to have had any value. The only way to have ensured this would have been to mark the quadrats permanently, which while desirable, was not practical for this study.

All woody and herbaceous species were counted and identified, and woody species were classified structurally as emergent, canopy, understorey, sapling or seedling. Although classification was based on height categories, flexibility and the observer's discretion were used, as the height of the forest canopy was by no means constant from quadrat to quadrat or even within quadrats. Thus a tree which may have been placed in the understorey in one quadrat, may have been classified as a canopy species in another. Quadrats were subsampled for seedlings, which were sampled in one quarter of each of the quadrats, giving a 100m² seedling sample per quadrat.

Height categories for the structural classification were as follows:

Seedlings: 0 - 49 cm

Saplings: 50 cm - 1.99 m

Understorey: 2 m up to the bottom of the canopy

Canopy: trees forming part of the canopy

Emergent: Trees protruding above the canopy

These categories were derived by conducting field trials to establish which categories were most easy to work with in terms of consistently separating forest vegetation into five reasonably distinct strata. While the established categorisations of Geldenhuys et al.(1988) were considered, these were not found to be practical in this regard in field trials.

For all woody species, a cover value was obtained by measuring the longest axis through the canopy and multiplying it by the longest axis at right angles to this axis. This provides a rough, standardized indication of the length and depth of the canopy. It is felt that this gives a better indication of the overall cover of the canopy than would be gained by multiplying the length of the canopy by its breadth.

Cover was not recorded for seedlings as this was not practical. Seedling numbers were recorded.

Non-woody plants were identified and classified as either lianas, ferns, undershrubs, geophytes, grasses or herbs according to Dyer (1976).

7. Sampling

"The world makes a messy laboratory for ecologists"
---Gleick, 1988 ---

"Order, Disorder, Entropy, Randomness - these
words are notorious traps"
---Gleick, 1990 ---

Central to the idea of sampling is the assumption that there is an underlying structure in vegetation that will reveal itself under appropriate sampling designs, such that patterns and associations in vegetation will be elucidated and subsequently clarified. i.e. the assumption of uniformity that can be characterised with a singular descriptive approach.

Sampling theory is replete with statistical considerations of scale e.g. Kershaw (1980), Rutherford and Westfall (1986), Werger (1972), Van Laar and Lewark (1973). In the study of disturbance, however, the role of the observer in defining scale, or choosing the level of resolution at which disturbance is to be characterised, cannot be ignored (Bazzaz and Sipe, 1987). Neither are disturbance events quantifiable in an absolute sense, but can only be meaningfully spoken of relative to the organisms which perceive them (Lieberman *et al.*, 1987). In many instances, the effects of disturbance cannot be sampled; often, disturbances, and their consequences, are events rather than ongoing fixtures in the environment. Even if disturbance can be described and characterised at a particular spatial scale at one locality, the critical correlation of disturbance effects with area (see Pickett and Thompson, 1978) mitigate against similar sampling approaches being successful when used in other areas. Rigidly prescriptive approaches (e.g. Rutherford and Westfall (1986)), their other limitations aside, are of little use in the variously sized, dynamic, and disturbed patch-structured environments found in Durban (this idea is expanded on in sections 20.2. & 20.2.2.).

In assessing the effects of past and present disturbance regimes on community structure and composition, and in attempting to compare forests to discover how different disturbance histories are expressed (see section 1.), one must take into account that generalisations about disturbance across different scales and community types encounter difficulties (Bazzaz and Sipe, 1987), (see sections 20.2. & 20.2.2.). Given the many differing degrees and types of disturbance, disturbance gradients, ways in which vegetation may respond to disturbance (floristically, physiognomically), natural environmental gradients which are either difficult to detect or have been altered by disturbance, and the unknowability of the 'ghost of disturbance past', it follows that both sampling and interpretive procedures need to be versatile. The reflection of disturbance history in the

structural arrangements and species compositions of tree populations is not always visually obvious to the untrained eye, and nor is the type, timing and intensity of disturbance being reflected. Furthermore, there are no reference points to consult in order to get an idea of what undisturbed coastal forest really should look like, assuming it should look like anything recognisable at all!

Where the effects of disturbance are visually arresting or obvious, or where one encounters forest one assumes to be in a near pristine state, the information to be gleaned from sampling is lessened. The reason for this is that one does not simply wish to describe a disturbance *per se*, and nor does one wish to describe 'undisturbed' forest. One in fact wishes to sample vegetation which one knows has been disturbed, and in which the 'response' to this disturbance is already being reflected. Structurally and floristically, in order that one may gauge what this response is. By sampling in such a way, one is also describing (albeit only at one spatial scale) the mosaic nature of the forest, in terms of its response to disturbance. This point; that one is only describing elements of a mosaic, as opposed to trying to describe the average characteristics of the forest, is important. In most instances, Durban forests are too small and disturbed for such homogeneity, or average characteristics, to exist. One is thus put into a position of having to site quadrats on the basis of a subjective decision regarding what constitutes such forest i.e. that which is neither 'pristine' nor too disturbed. Conventional methods for siting quadrats do not work in such instances. In forests with high internal heterogeneity the random siting of quadrats may lead to quadrats being placed in inappropriate areas e.g. open patches, paths, areas dominated by exotics in which there is no natural vegetation. Individual quadrats may also be placed such that they include areas which are so different that the average of the information collected within them would be meaningless. These constraints are exacerbated by the small size of the forests concerned e.g. in Pigeon Valley (10 ha) it was difficult to site four quadrats such that they were all in relatively homogenous areas of forest. Stratification of any sort is difficult in the absence of specific knowledge regarding past distributions and times of disturbance events in the particular forest concerned. Given the different scales at which disturbances can be characterised, and the multiplicity of possible vegetation responses (see section 21.), this information could only ever be known in the crudest of ways.

Furthermore, one is attempting to study man-induced disturbance in an environment which, to some extent, is maintained by natural disturbance, while at the same time one is attempting not to confuse the two. Plants however, are integrators of their disturbance history, irrespective of what has caused it. Ideally, one should know how a forest has been disturbed prior to one's sampling attempt. However, given the subtleties and vagaries of how disturbance may be reflected in the vegetation's response, this information would need to be very detailed, and collecting it would pose distinct methodological challenges.

This idea is taken up in Parts 2 and 3 as one of the themes of this thesis.

In this study, quadrats were sited in physiognomically homogenous areas of forest, an attempt being made to:

1. encompass areas reflecting one disturbance type per quadrat.
2. choose different areas in order to sample a range of different vegetation responses to disturbance in forest which appeared to display some degree of recovery to disturbance.

As a result of the sampling approach:

1. the results of data analyses are seen as possible hypothesis generators rather than as answers in themselves.
2. results are to be seen as tentative, and the descriptive content of the information collected is seen as being important in itself.

Ordinations were not used to elucidate environmental gradients and community types but in order to establish how plants are integrators of their specific disturbance environments. Ordination procedures are useful for descriptions of the results of environmental perturbations (James and McCulloch, 1990). In this study indirect ordinations (James and McCulloch, 1990) were performed. This entails the analysis of a matrix of data for the presences and absences of species in each stand, with their actual or relative density, biomass or cover as the attributes. In this study, actual cover values were used. The objective is to find a systematic pattern of relationships among the stands based on the co-occurrences of their component species (James and McCulloch, 1990). Ordinations were performed for four of the five structural classes, emergents being left out on account of there being too few trees in this class. This approach has been used with seeming success by Hobbs (1988) in analysing variations in the structure and composition of urban forest islands, as well as successional trends occurring therein (see results).

Environmental data were not collected in this study. In the highly altered urban environment it is suspected that subtle, hard to detect environmental gradients, even if they were measurable, would be overridden by disturbance-induced and/or mediated gradients and ensuing small scale phenomena of secondary succession (this idea is clarified in sections 19.7. & 20.2.2.1.).

The overriding effect of disturbance in forests is to alter microclimate, and it is likely that plants respond to microclimate primarily, and to environmental gradients secondarily. Certainly it is true that disturbance, and its effect on microclimate, would confound the already difficult interpretation of vegetation response to environmental gradients. It is arguable, too, whether such information would be of real value, as disturbance-initiated trajectories are maintained as

trees grow, while environmental determinants are more specifically operative for young plants, i.e. it takes a long time for past disturbance effects to be overridden.

One is trying to describe the degree of patchiness in a patch-structured environment, not to elucidate pattern from seeming homogeneity as in classic phytosociology.

What one sees depends on how one samples, and what one samples depends on what one is looking for.

8. Results

"Perhaps the training of ecologists requires more emphasis on the large temporal and spatial scale arts and sciences, such as geology, geography, history, and even the better quality science fiction, and less emphasis on ever more sophisticated statistical methods for fine-tuning the answers to temporally and spatially coarse-grained questions"
 --- Green, 1983 ---

8.1. General Comments

I wish to make it clear from the outset that the repeated references to Mr. G.R. Nichols in this section serve a specific and important purpose. This is to indicate that the potential usefulness of the data is significantly enhanced by the insights and skills of a good naturalist and observer who has an historical interest, as well as long-standing and ongoing field experience in the areas investigated. In my judgment the interpretations arrived at are correct and I can corroborate Mr. Nichol's ideas. It is unlikely, however, that all of them could have occurred to me had I interpreted the data alone.

This section is thus intended not only to analyse the data but to provide a factual basis for parts of this thesis which are to follow.

Urban forests are products of the pre-urban environment, the contemporary environment, and the processes of disturbance which have accompanied urbanisation (Hobbs, 1988), and, presumably, those which continue to do so. Insights into their present conditions and future trends can be gained by using ordination (Hobbs, 1988). In such unstable vegetation it is important to add understorey species to the ordination as they have shorter histories and may be better indicators of current environmental conditions and ongoing successional processes than mature trees (Hobbs, 1988). Hobbs (1988) used ordinations to analyse variations in the structure and composition of urban forest islands in Minnesota, which revealed compositional gradients varying from gradients described for non-urban forests in the same region, suggesting that different successional trends were occurring there. Hobbs (1988) found that these ordinations were improved through the addition of saplings, shrubs and herbs to the analysis.

In this study, ordinations were performed on the data for each structural class for the reasons cited above, and in order to put the quadrats on a comparable basis. Emergent species were not ordinated because there were too few to provide an interpretable analysis. In addition to the four structural classes ordinated,

climbers, climber/trees, ferns, grasses, geophytes, scramblers, herbs, shrubs, undershrubs, parasites, xerophytes, palms and weeds (according to Dyer, 1976) were recorded. A record of the species in these various classes is provided in sections 8.7.1. to 8.7.5.. Given the difficulties in interpreting the ordinations, and the generally low numbers of non-woody species, it was not felt that adding non-woody species would have clarified the ordinations.

Ordinations were based on both species and a structural attribute, in this case cover, because forest structure, often more than species composition, determines the value of a forest as a habitat (Hobbs, 1988). Furthermore, it is assumed that disturbance is reflected both structurally and floristically. For this reason, as well as being an attempt to quantify within-forest heterogeneity, Figs. 6 - 10 are submitted to show within-forest quadrat differences and Figs. 11 and 12 are submitted to demonstrate the variation in absolute cover values and tree numbers for each structural class per forest (for the purposes of comparison these Figures appear together at the end of section 8.5.). Such variation is evident even after the averaging effect of summing values from four quadrats per forest. Numbers of seedlings were not considered as these are transient in the environment, and survivorship is unknown.

It is important to note that the ordinations performed were "indirect ordinations" (James and McCulloch, 1990) in that the data were analysed for presences and absences of species in each stand, and their cover as attributes. The objective of indirect ordinations is to find a systematic pattern of relationship among stands based on the co-occurrences of their component species (James and McCulloch, 1990) which may subsequently be related to environmental or disturbance factors.

8.2. Seedling ordination

The seedling ordination is presented as Fig. 2. SNR4 and BB2 do not appear as no seedlings were recorded in these quadrats. Immediately notable is the clumping of Virginia Bush (VB) quadrats at the seedling level. The association of individual quadrats at this level indicates a consistent regeneration response among the four quadrats, both in number (see Fig. 9) and in species makeup as suggested by the ordination itself. The suggested consistent makeup of the seedling population among quadrats explains the general grouping of VB quadrats in all structural classes, and underlies the consistently particular floristic response VB demonstrates to what was a homogenous historical disturbance. At the seedling level the VB grouping is accounted for by *Apodytes dimidiata*, *Allophylus natalensis*, *Antidesma venosum*, *Canthium inerme*, *Canthium spp.*, *Scutia myrtina*, and *Teclea gerrardii*.

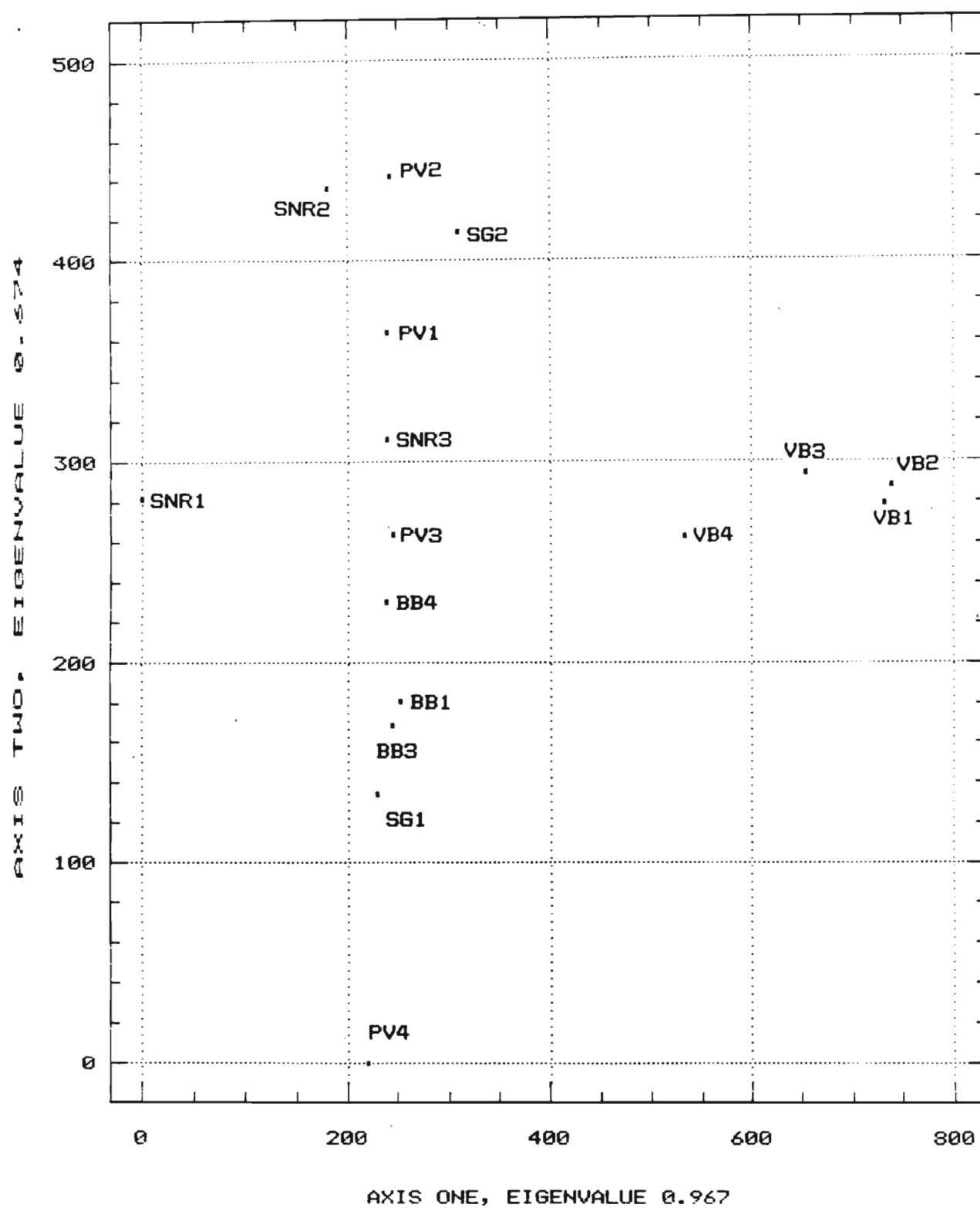


Figure 2 : DCA ordination of seedling species for Durban forest sites.

These are all pioneer species and strong regenerators (Nichols pers. comm.) and *Teclea gerrardii*, a dune forest dominant, reflects the proximity of the nearby dune forests of Umhlanga and Hawaan (Nichols pers. comm.).

The separation of one of the Stainbank Nature Reserve (SNR1) quadrats on axis one is accounted for by *Drypetes* spp. and *Hyperacanthus amenus*. Thirty five years ago the present Stainbank Nature Reserve was a grassland community with scattered bushclumps where it is likely that *Drypetes* populations were confined to undisturbed cliff communities bordering the river (Nichols pers. comm.). *Drypetes* is slow growing and cannot be considered a pioneer species, and its presence suggests that the slopes above the river have remained relatively undisturbed for some time (Nichols pers. comm.). The high numbers of *Drypetes* in this area can be explained in terms of their highly palatable fruits which are dispersed by birds, monkeys and buck (Nichols pers. comm.). Stainbank is known for its high populations of Bushbuck and Duiker, suggesting a reason for why *Drypetes* has been successful in spreading from the cliff communities and onto the upper slopes (Nichols pers. comm.). It is possible that the same explanation can be invoked to understand the grouping of SNR1 and BB1 and 3 on the sapling ordination, as these three sites also have particularly high numbers of both *Drypetes* spp. and *Drypetes arguta*. *Hyperacanthus amenus* fruits are sought after by monkeys, possibly accounting for their seemingly strong regeneration in these areas (Nichols pers. comm.).

In general, the seedling community appears a relatively undifferentiated one with little separation along the first axis with its high eigenvalue of 0.967. The large grouping is accounted for by species such as *Acokanthera oblongifolia*, *Anastrabe integerrima*, *Baphia racemosa*, *Bequaertiodendron natalense*, *Calodendrum capensis*, *Carissa bispinosa*, *Chaetacme aristata*, *Chrysophyllum viridifolium*, *Cryptocarya woodii*, *Deinbollia oblongifolia*, *Drypetes arguta*, *Rhus chirindensis*, *Rothmania globosa*, *Sapium integerrimum*, *Strychnos usambarensis*, *Syzygium cordatum*, *Uvaria caffra*, *Vepris lanceolata* and *Vitellariopsis marginata*. This generalised grouping consists mainly of species whose fruits and seeds are dispersed by monkeys and birds, exceptions being *Anastrabe integerrima* which has wind dispersed seeds, and *Baphia racemosa* whose dispersal is mechanical (Nichols pers. comm.). The reason for mentioning this is that it suggests the importance of birds in effecting the distribution and recolonisation of species, especially among small isolated forests between which birds travel. The species makeup of birds in the forests with which this thesis has been concerned is subject to definite fluctuation (Nichols pers. comm.) and this may both affect, and be affected by management actions. In general, these species may be considered as intermediate between early successional or disturbed forest situations and mature undisturbed forest situations (Nichols pers. comm.).

Some differentiation in the seedling community is suggested, however, by the second axis with Stainbank (SNR2), Pigeon Valley

(PV2) and Silverglen (SG2) quadrats having *Bequaertiodendron natalense*, *Canthium spinosum*, and *Euclea natalensis* (SNR2 & SG2) in common at one end of the gradient while PV4 is distinctive in having *Chrysophyllum viridifolium* and *Deinbollia oblongifolia* at the other. Given the level of sampling intensity however, it is difficult to interpret such occurrences. The existence of PV quadrats at both extremes as well as at an intermediate position on axis 2 as well as the lack of any significant groupings (apart from VB) on axis one, however, suggests a floristically homogenous nature for seedling communities in general with some within-forest differentiation on the second axis.

Overall, the seedling ordination suggests a gradation in species makeup from pioneer species in VB on the right of the ordination to species reflecting intermediate levels of maturity or disturbance in the middle to those indicative of undisturbed forest on the left of the ordination.

8.3. Sapling ordination

The sapling ordination is presented as Fig. 3. BB2 was removed from the ordination as it contained only two individuals from two species, one of which (*Chaetacme aristata*) was found only in BB2. BB2 thus obscured the remaining quadrat scores. The VB grouping is most obvious and, with the exception of *Teclea gerrardii* is accounted for by the same species as those accounting for the separation at the seedling level. Other species accounting for its separation are *Albizia adianthifolia*, *Brachylaena discolor*, *Bridelia micrantha*, *Calpurnia aurea*, *Canthium spinosum*, *Capparis* spp., *Clerodendrum glabrum*, *Deinbollia oblongifolia*, *Erythrina lysistemon*, *Erythrina* spp., *Eugenia capensis*, *Eugenia uniflora*, *Ficus natalensis*, *Harpephyllum caffrum*, *Litsea glutinosa*, *Maytenus procumbens*, *Melia azedarach*, *Morus alba*, *Pavetta lanceolata*, *Psydrax obovata*, *Rhus nebulosa*, *Rhus pentheri*, *Sapium integerrimum*, *Schinus terebinthifolius*, *Strelitzia nicolai*, *Syzygium cordatum*, *Syzygium cuminii*, *Trema orientalis*, *Tricalysia sonderana* and *Vangueria infausta*.

Rhus nebulosa, *Psydrax obovata*, *Eugenia capensis*, *Maytenus procumbens*, *Tricalysia lanceolata* and *Brachylaena discolor* are primary dune forest species, again suggesting the proximity of the dune forests of Hwange and Umhlanga. Also notable is the high number of fruit-bearing aliens such as *Litsea glutinosa*, *Melia azedarach*, *Schinus terebinthifolius* and *Syzygium cuminii*, all of which are much sought after by birds who transport the seeds into VB from surrounding gardens (Nichols pers. comm.).

Three of the four PV quadrats (PV1, 2 & 3) are loosely grouped with *Bequaertiodendron natalense*, *Celtis mildbraedii*, *Cussonia* spp., *Lagynias lasiantha*, *Millettia grandis*, *Ochna natalitia*, *Oxyanthus pyrifolius*, *Pavetta inandensis*, *Rawsonia lucida*, *Rhus* spp., and *Trichilia dregeana* accounting for their association.

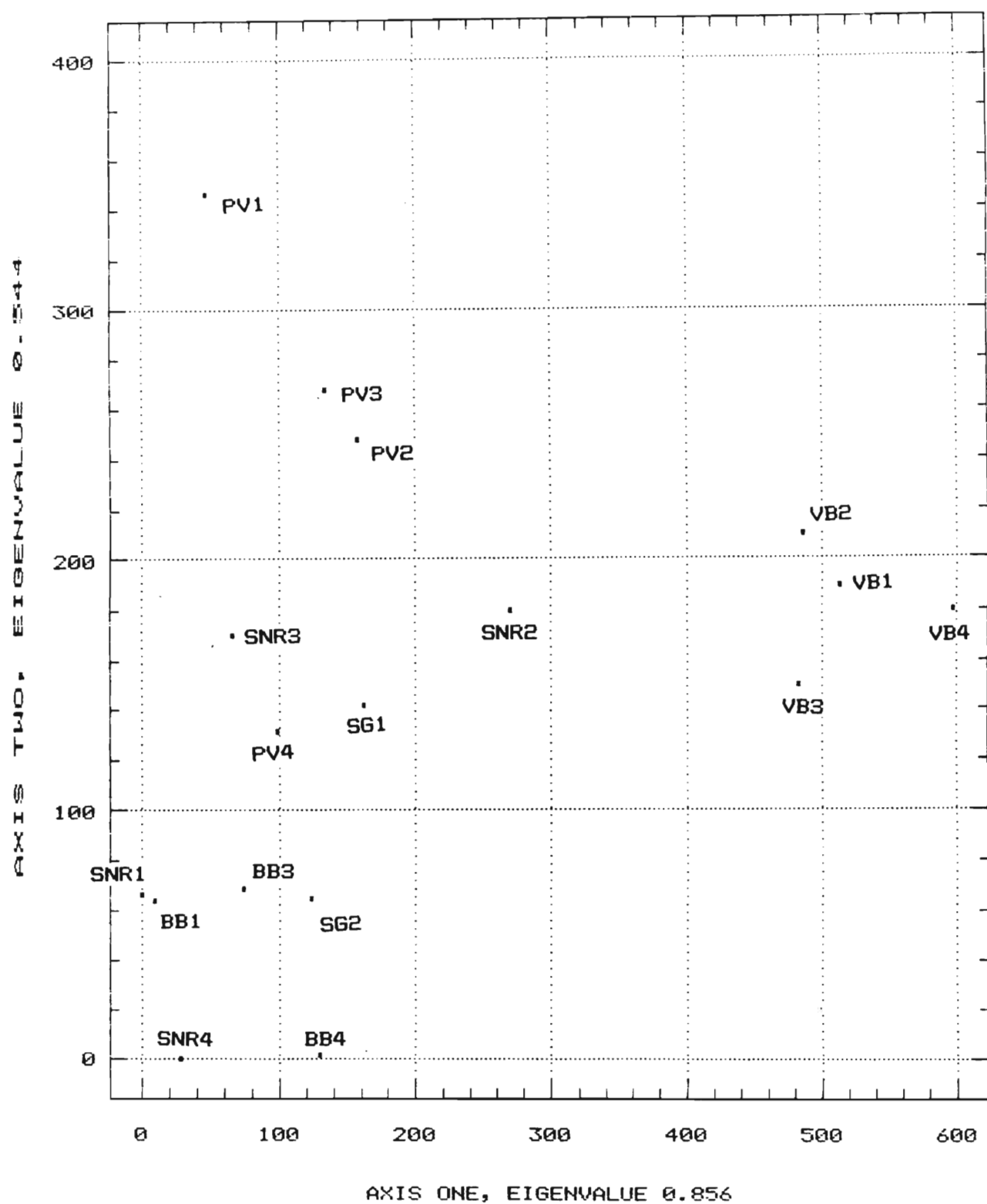


Figure 3 : DCA ordination of sapling species for Durban forest sites.

It is notable that a *Millettia grandis* tree was in fact planted in VB in the 1960s (Nichols pers. comm.), and that the *Millettia* sapling recorded in this quadrat may be a descendent of that tree. There are no other *Millettia* trees in VB (Nichols pers. comm.). The presence of the rare *Celtis mildbraedii*, which is not found in any of the other forests, is a reflection of a disjunct distribution limiting it to very few Natal forests, rather than a reflection of disturbance factors (Nichols pers. comm.).

The presence in this grouping of *Oxyanthus pyriformis*, *Pavetta inandensis* and *Rawsonia lucida* is notable as they are all rare, mature forest species (Nichols pers. comm.). Their presence in PV reflects the fact that small populations were maintained there throughout a history of disturbance, including the invasion of exotics and construction of a stormwater drain through the middle of the park. In addition to this, PV is both small, and isolated from other forests. In the mid 1960s to late 1970s 25% of PV was covered by the aliens *Chromolaena odorata* and *Lantana camara* which invaded traditionally mowed areas (Nichols pers. comm.). This process created an ecotone which attracted birds such as Gorgeous Bush Shrikes, White-Bellied Sunbirds and Yellow-Bellied Bulbuls (Nichols pers. comm.). This increase in bird diversity is possibly significant in explaining the high numbers of *Oxyanthus pyriformis*, which is bird dispersed, as well as the maintenance of both *Rawsonia lucida* and *Pavetta inandensis*, also bird dispersed species, in the sapling layer (Nichols pers. comm.). The high numbers of *Oxyanthus pyriformis* recorded also reflect the fact that it produces lots of seed, is seldom parasitised, and regenerates in low light conditions, enabling it to regenerate beneath the alien invasive *Chromolaena odorata* prior to 1986 when this species was eradicated through management efforts (Nichols pers. comm.).

The three loose associations of SNR3, PV4, SG1; SNR1, BB1, BB3, SG2 and SNR4 and BB4 can probably not be profitably further explored in light of the low eigenvalue (0.544) for this axis and the inconsistent mixture of quadrat groupings from different forests. Notable, however, are the large numbers of *Baphia racemosa* in BB1 and 3, although this is not directly suggested by the ordination species scores. BB1 and 3 are sited on fairly wet areas where it is natural to find large numbers of *Baphia* (Nichols pers. comm.). This observation is confirmed in the occurrence of similarly large numbers in wet areas in Stainbank, Empasini and the Illanda wilds (Nichols pers. comm.).

8.4. Understorey ordination

The understorey ordination is presented as Fig. 4.

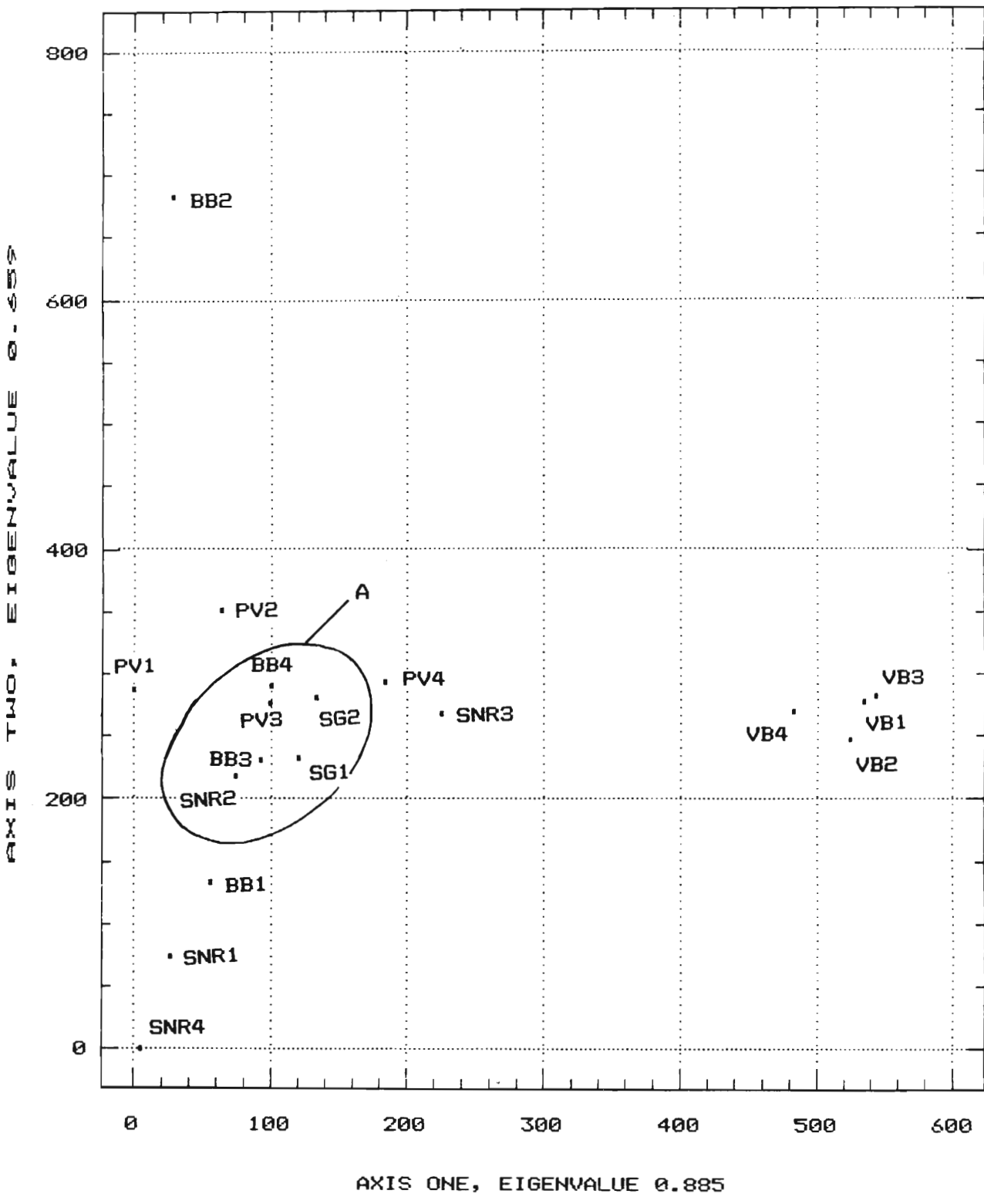


Figure 4 : DCA ordination of understorey species for Durban forest sites.

The VB grouping, again distinctive, is accounted for by *Antidesma venosum*, *Apodytes dimidiata*, *Brachylaena discolor*, *Bridelia micrantha*, *Carissa bispinosa*, *Clerodendrum glabrum*, *Erythrina* spp., *Eugenia capensis*, *Ficus natalensis*, *Grewia* spp., *Litsea glutinosa*, *Mimusops caffra*, *Sapium integerrimum*, *Scutia myrtina*, *Syzygium cordatum*, *Syzygium cuminii*, *Trema orientalis* and *Tricalysia sonderana*. With the exception of *Carissa bispinosa*, *Grewia* spp. and *Mimusops caffra* these are the selfsame species which have accounted for separation at the seedling and sapling levels. To some extent this overlap can be explained in that trees whose height is in the region of 50cm and 2m may fall into different structural categories although not appreciably different in height i.e. trees do not neatly fit into different structural/height categories but form a continuum. What this also suggests, however, is that the trajectory of recovery from disturbance has not changed markedly from when recovery began, with the same species regenerating beneath the canopy as those initially giving rise to the formation of the present canopy. The duneforest component is evident in the presence of *Eugenia capensis*, *Grewia* spp., *Scutia myrtina*, *Sapium integerrimum* and *Carissa bispinosa*, with the duneforest canopy dominants *Mimusops caffra* and *Erythrina* spp. also in evidence (Nichols pers. comm.).

Also notable is the separation of BB2, a structurally distinctive quadrat (see Fig. 6) which was characterised by *Allophylus melanocarpus*, *Commiphora* spp., *Cordia caffra*, *Cussonia zuluensis*, *Deinbollia oblongifolia*, *Hippobromus pauciflorus*, *Kraussia floribunda*, and *Turraea floribunda*.

Turraea floribunda, *Allophylus melanocarpus* and *Commiphora* spp. are mature forest species associated with undisturbed habitats (Nichols pers. comm.). Structurally, BB2 and SNR4 are similar (see Figs. 6 & 7), both displaying a structure reminiscent of mature undisturbed forest (Nichols pers. comm.).

The association of SNR, BB, SG and PV quadrats (shown as A) is due to the following relatively common species: *Acalypha glabrata*, *Baphia racemosa*, *Bersama lucens*, *Celtis africana*, *Clausena anisata*, *Croton sylvaticus*, *Cryptocarya woodii*, *Drypetes arguta*, *Hyperacanthus amenus*, *Protorhus longifolia*, *Putterlickia pyracantha*, *Rothmania globosa*, *Sideroxylon inerme*, *Strychnos madagascariensis*, *Tecomaria capensis* and *Vepris lanceolata*.

The grouping of SNR4 and SNR1 on axis one and two is an artefact of the DECORANA procedure as they are structurally different (see Fig. 7) and have only one species (*Drypetes* spp.) in common. SNR4 is distinctive in having a specimen of *Scolopia zeyheri*, but otherwise has a 100% cover of *Isoglossa woodii*. This was not entered into the ordination as it would have caused SNR1 to appear as an outlier while distorting its floristic relation to other quadrats. The presence of only two individuals in the understorey of this 'undisturbed' quadrat may reflect the unusually high numbers of duiker and bushbuck, which exert extremely heavy grazing pressure on the forest understorey (Nichols pers. comm.).

The presence of *Wrightia natalensis* and *Pavetta lanceolata* in SNR1 and *Scolopia zeyheri* in SNR4 is indicative of an undisturbed state (Nichols pers. comm.), confirming the separation of SNR1 on this basis in the seedling ordination. The numbers of these species in the understorey is however very low (only one of each), suggesting the further inadequacy of DECORANA in making useful separations at this level of sampling and in such an unhomogenous environment.

8.5. Canopy ordination

The canopy ordination is presented as Fig. 5. PV1 was removed from the ordination as it was the only quadrat out of all canopy quadrats to contain *Celtis mildbraedii*, causing it to obscure the distribution of the remaining canopy quadrat scores. The VB grouping (labelled A) is again evident, and reflects the association of *Antidesma venosum*, *Bridelia micrantha*, *Melia azedarach*, *Syzygium cuminii* and *Trema orientalis*.

This predominance of these species reflects both the dune forest component present in the other structural layers as well as the isolation of VB from other forests and other sources of propagules (Nichols pers. comm.). Although mainly exotic and generalist species predominate, this species makeup is favourable for birds and for this reason is considered desirable at present (Nichols pers. comm.). Injudicious removal of exotic species can result in subsequent loss of bird species as witnessed by the departure of Purple Crested Loeries following the mass removal of *Melia azedarach* from Pigeon Valley (Nichols pers. comm.).

The SNR grouping (labelled B) reflects the presence of *Bequaertiodendron natalense*, *Cassipourea gummiflua*, *Combretum molle*, *Croton sylvaticus*, *Hyperacanthus amenus*, *Millettia grandis* and *Ptaeroxylon obliquum* in SNR1 and *Vepris lanceolata* and *Bequaertiodendron natalense* in SNR2. *Cassipourea gummiflua*, a species associated with wet habitats, was in fact planted in Stainbank and possibly does not occur there naturally (Nichols pers. comm.).

BB2 is distinctive, both structurally (see Fig. 6), and floristically in having *Celtis africana*, *Maytenus heterophylla* and *Olea woodiana*.

Structurally, BB2 is reminiscent of SNR2 & 4. Although they are characterised by *Bequaertiodendron natalense*, *Chaetacme aristata*, *Strychnos madagascariensis* and *Vepris lanceolata* in SNR2 and *Anastrabe integerrima*, *Brachylaena* spp., *Chaetacme aristata* and *Maytenus peduncularis* in SNR4, all three of these quadrats are characterised by high canopies with very little recorded in the sapling and understorey layers (see Figs. 6 & 7).

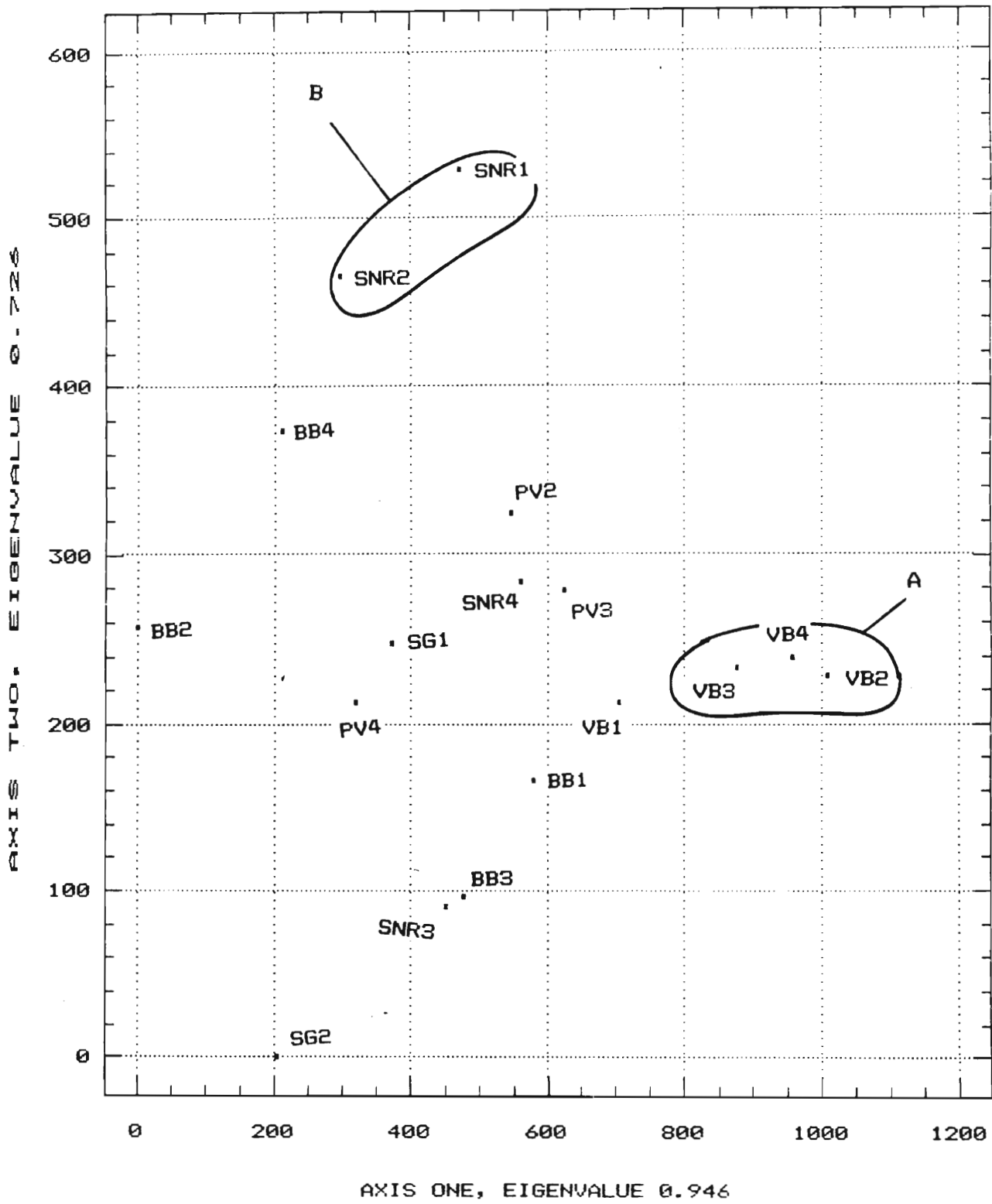


Figure 5 : DCA ordination of canopy species for Durban forest sites.

Given the disturbance history of Stainbank, which was farmed and grazed, and was primarily grassland as late as the 1930s (Nichols pers. comm.), it is likely that these patches, reminiscent of healthy climax forest, may be the centres of either remnant bushclumps or larger forest patches which were left undisturbed (Nichols pers. comm.). This idea is substantiated in the structure of BB2, a small patch reminiscent of undisturbed forest (Nichols pers. comm.).

The presence of *Chaetacme aristata* in the canopy of all sampled forests (with the exception of VB) highlights the fact that disturbance may leave some species unaffected. *Chaetacme* is a late successional species found in many of the older, less disturbed Natal forests (Nichols pers. comm.), and its presence in Durban forests possibly provides a clue to their less disturbed pasts.

SNR3 is floristically similar to BB3, although they are structurally different (see Figs. 6 & 7), suggesting disturbance in the lower layers of the forest.

At the other end of the gradient (axis 2) SG2 is distinctive in having *Protorhus longifolia*, *Psydrax obovata*, *Rhus chirindensis*, *Schotia* spp., *Scolopia zeyheri* and *Strelitzia nicolai*, with the rest of the canopy community being undifferentiated at the scale of investigation.

Despite only having two quadrats, Silverglen has a higher species diversity than the other four localities, confirming it as one of the richest forests in Natal (Nichols pers. comm.). SG2 was placed on a site which was disturbed when as many as 10 000 people occupied the area during the construction of the Clearwater dam in 1901 when it was probably a fire-maintained grassland (Nichols pers. comm.). The occurrence of *Protorhus longifolia*, *Rhus chirindensis* and *Psydrax obovata* in this quadrat reflects the early successional nature of the trees which would have occupied the site subsequent to the construction of the dam, and which now occupy the canopy. This recovery may reflect the fact that this area has been undisturbed since the completion of the dam which is protected by the Durban Corporation (Nichols pers. comm.). In contrast to SG1, the low number of seedlings in SG2 may reflect the fact that a fire recently penetrated the forest patch where SG2 was sited (Nichols pers. comm.).

It is interesting to note that even the area below the dam wall where much of the rock excavated from the dam during its construction was dumped, has now recovered and has a high species diversity, including some rare species with highly localised distributions (Nichols pers. comm.). This seeming relationship between diversity and disturbance is further suggested by Nichols (pers. comm.) who maintains that diversity in Silverglen has been enhanced by recent burning in the area with the result that many bushclumps that may otherwise have developed into forest have been kept open.

SG1 was sited in a relatively undisturbed forest patch (Nichols pers. comm.) where, albeit unreflected in the ordination, its high species diversity and number in all structural classes make it a distinctive piece of forest. Its mixture of early successional species such as *Baphia racemosa*, *Bequaertiodendron natalense*, *Psychotria capensis*, *Rothmania globosa*, *Uvaria caffra* and *Xylothea kraussiana* as well as later successional species such as *Hyperacanthus amenus*, *Maytenus peduncularis* and *Cryptocarya woodii* make it a food-rich habitat for birds. This is significant in that this patch and the surrounding area provides habitat for uncommon species such as Green Coucals, Grey-headed Bush Shrikes and Narina Trogons (Nichols pers. comm.).

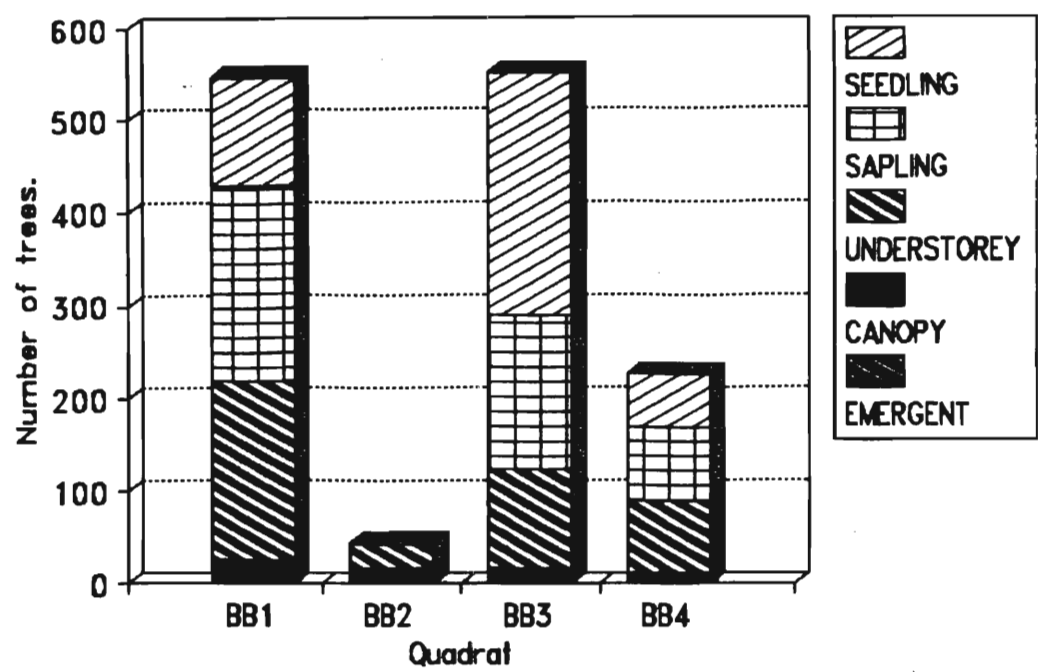


Figure 6. : Structural class breakdown per quadrat for tree numbers in Burman Bush.

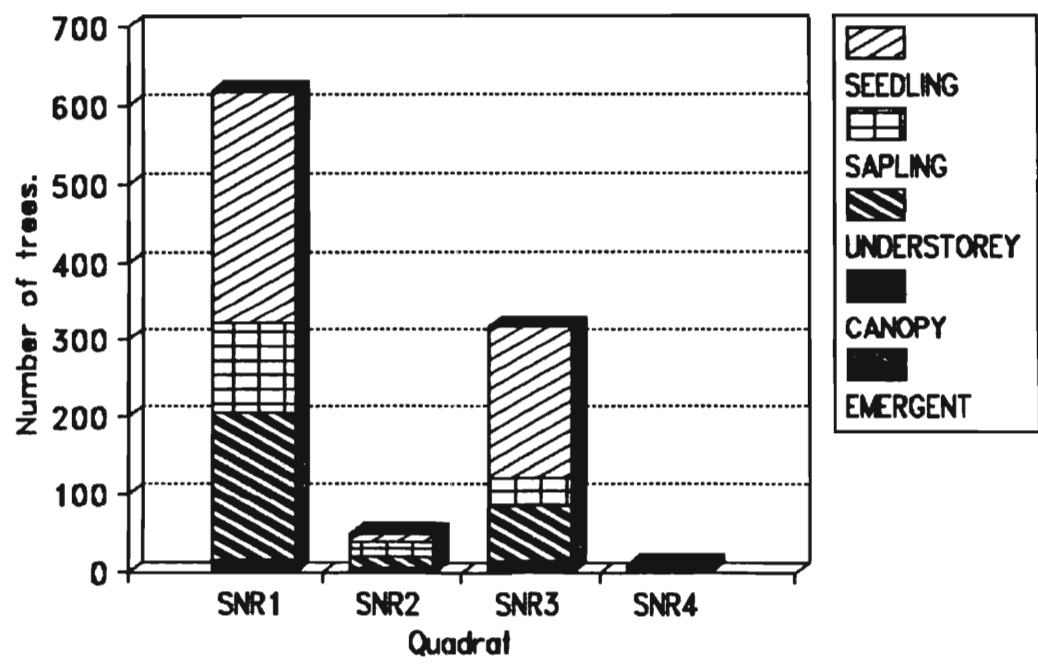


Figure 7. : Structural class breakdown per quadrat for tree numbers in Stainbank Nature Reserve.

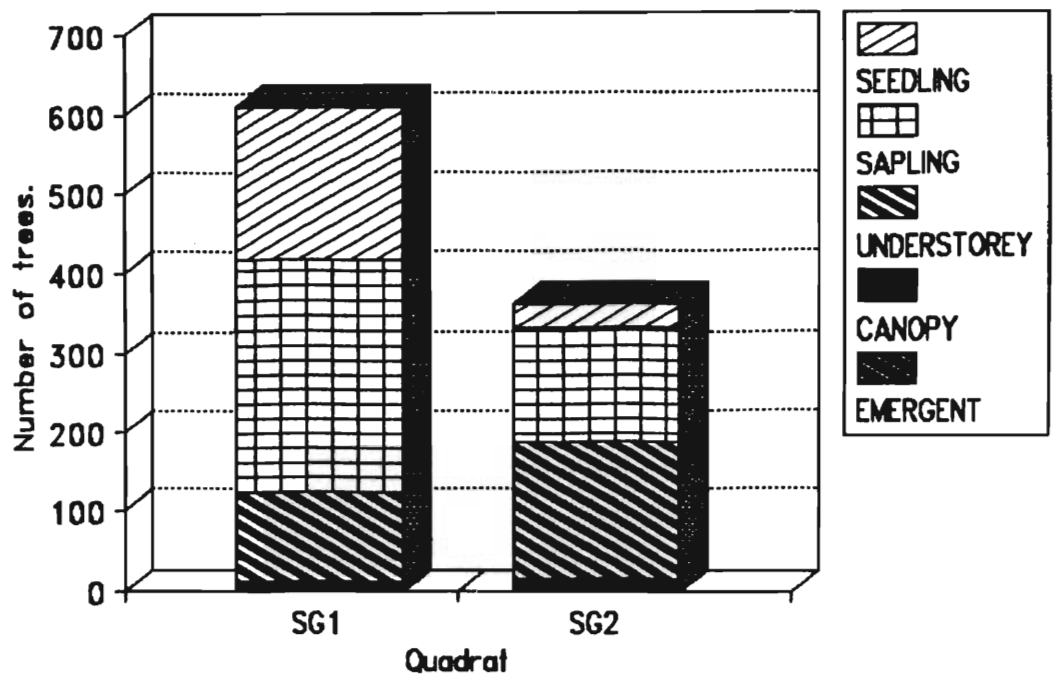


Figure 8. : Structural class breakdown per quadrat for tree numbers in Silverglen Nature Reserve.

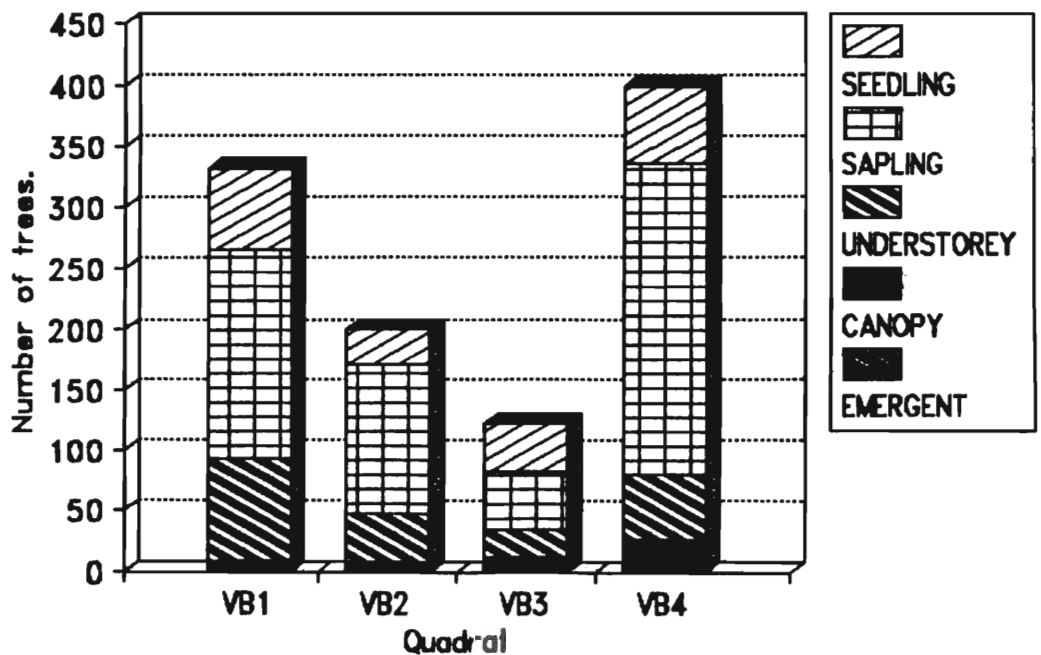


Figure 9. : Structural class breakdown per quadrat for tree numbers in Virginia Bush.

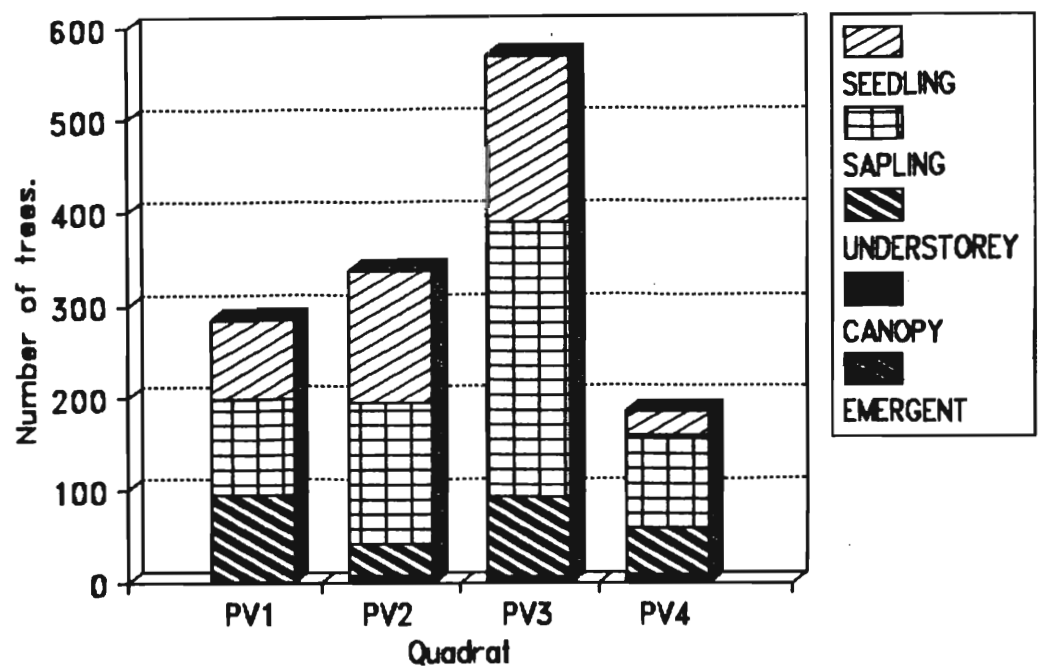


Figure 10 : Structural class breakdown per quadrat for tree numbers in Pigeon Valley.

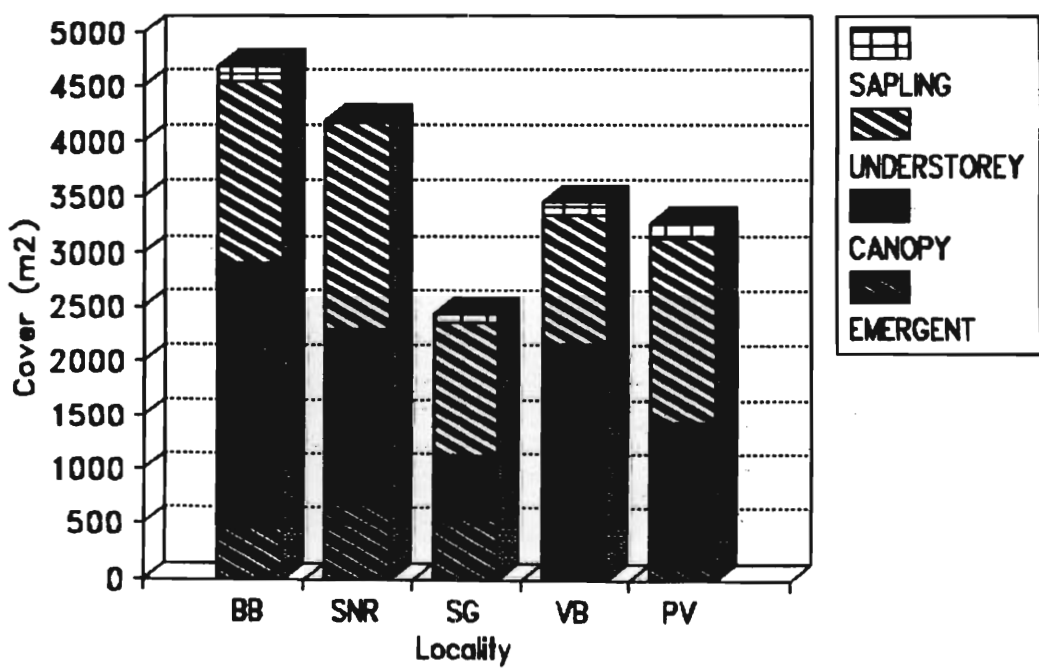


Figure 11. : Summed absolute cover values per structural class for each of the five forests.

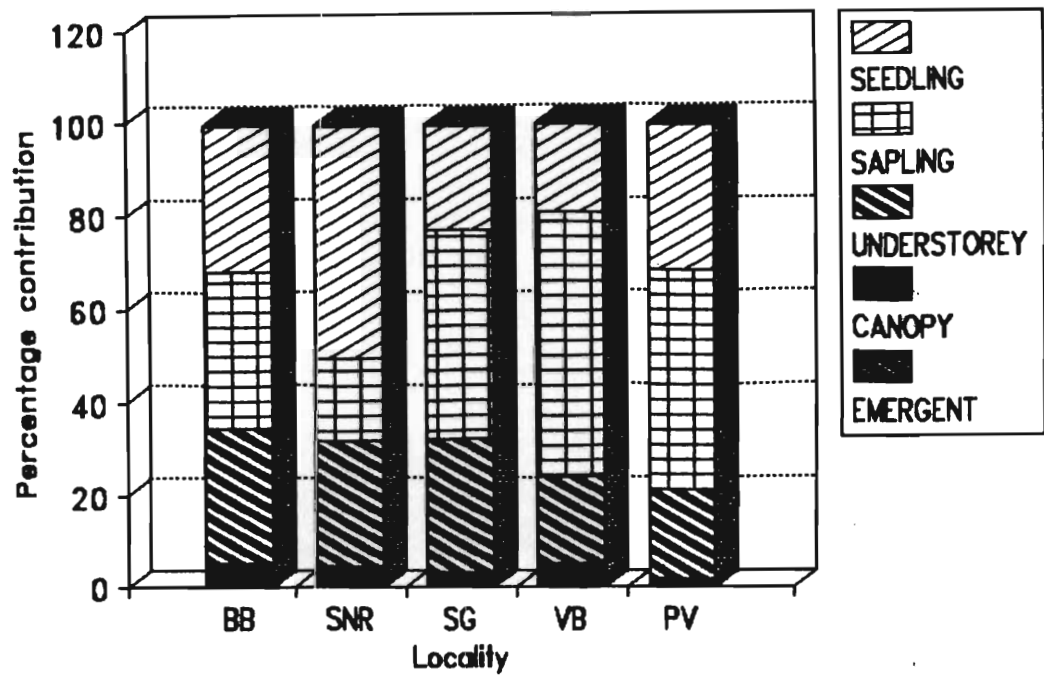


Figure 12. : Contribution to the total number of trees, calculated as a percentage per structural class for each of the five forests.

8.6. Conclusions

Forest disturbances following urbanisation are conceivably different from those to which forests had become adapted before (Hobbs, 1988) and the processes of change occurring in these forests, and their ultimate composition may be unprecedented (McCune and Cottham, 1985 in Hobbs, 1988). Kaesler *et al.* (1974) and Macdonald and Green (1983) in Green (1983) state with respect to multivariate statistical approaches that there is usually high redundancy among biological variables in the information they contain about spatial and temporal structure of both natural and impacted communities. Given that Durban forest communities may recently have been subject to unique spatial and temporal stresses, the expected presence of the arch effect in indirect two-dimensional ordinations (James and McCulloch, 1990) and the inability of DECORANA to discover nonlinear relationships (James and McCulloch, 1990), it is to be expected that at least some of the pattern generated will be an artefact of the procedure used. This possibility is particularly likely when there are two independent gradients of variation in the data (Hill and Gauch, 1980). If the longer gradient is shortened by the removal of samples that are more extreme on it (as occurred in the sapling and canopy ordinations), then there will come a point when the dominant eigenvector does a quantum jump, and flips to the other independent direction of variation (Hill and Gauch, 1980). Care is thus needed in comparing analyses of differing subsets of a large data set because depending on which axis is considered, the same gradient can be represented as axis 1 or a higher axis, or can have its direction reversed (Hill and Gauch, 1980). As Hill and Gauch conclude their paper on DCA, "the interpretation of results remains a matter of ecological insight and is improved by field experience....."

As a result, tendencies to overinterpret the data have been resisted, as the assignment of causation in the absence of experimentation carries implications about causal relationships and has been strongly criticised by James and McCulloch (1990). Goldstein and Grigal (1986) suggest that because ordination methods are strictly mathematical, they are valid regardless of the statistical properties of the system which in any event can generally not be established for ecological systems. These authors state that where statistical inferences are not possible, results should be interpreted in a qualitative manner to gain insights into the system, to generate meaningful hypotheses, and to design experiments to test these hypotheses. This conclusion will argue that disturbance-induced environmental heterogeneity and the undetectability of any consistent disturbance response, either floristically, numerically or structurally, render the ordinations meaningless without qualitative interpretation. At worst, these factors conspire to suggest the presence of forest and quadrat-specific processes that cannot be summarised, reduced or interpreted as trends by multivariate analytical procedures. In itself, the detection of relationships implies that there are just a few of them, while the detection of trend implies linearity.

The changing nature of relationships between within-forest and between-forest quadrats suggests (tentatively) that patterns of heterogeneity within disturbance patches do change and are not predictable i.e. responses to disturbance do not proceed along knowable physiognomic or floristic trajectories. This reflects the stochastic nature of processes within individual plots, suggesting that the products of disturbance are unique, and that this is what makes forests forests. These patterns also suggest that although quadrats were chosen on the basis of physiognomic homogeneity, they are not necessarily comparable on this basis. This could be because what is deemed floristically or physiognomically homogenous by the observer may in fact reflect a multitude of disturbance events of differing frequencies, intensities and magnitudes, as well as the products of ongoing disturbance. If one considers response to disturbance (post-disturbance recovery) to follow certain pathways, then it is reasonable to expect that input into these pathways will vary according to surrounding species, pollinators, dispersal agents, degree of isolation from other forests and chance. Thus, contrary to prevailing belief, disturbance outcomes cannot always be retrospectively, or causally traced to specific events because they do not reflect specific causal instances. Disturbance patterns are neither wholly historical nor wholly of the present, and separating disturbance history from current ecological process is difficult. If this is the case, it suggests the appropriateness of management approaches that are based on observation and description as opposed to those based on quantification and comparison, as well as the need to monitor and describe individual within-patch processes. Even in VB where separation has been consistent, this consistency is primarily floristic rather than structural. This can be seen for instance in the fact that VB3 and VB4 group consistently close together on both the first and second axes despite their different structural characteristics (see Fig. 9). Thus, DECORANA has not provided appropriate cover-based quadrat separations despite the inclusion of cover in the input data. Other instances of this can be seen with respect to SNR2 and SNR1 (see Fig. 7), which, although appreciably different in structure for all four structural classes, have grouped consistently closely on axis one in all four ordinations. This shortcoming is compounded by, and may reflect the fact that the relationship between numbers of trees and their cover values is not a consistently clear one. For instance a closer analysis of the difference between VB3 and VB4 reveals substantially differing numbers of trees e.g. 74 saplings of *Apodytes dimidiata* in VB4 as opposed to 5 in VB3, with a difference in cover of only 5.1 m² as a result. Other similar examples do occur.

The fact that quadrat separations for the four structural classes vary with each ordination suggests that structural character does not reflect particular species associations, i.e. a particular structural arrangement does not imply the presence of certain species. This suggests the difficulty of describing or sampling for a particular response to disturbance in terms of either one. It is also possible that attempts to quantify different

structural attributes in forests would be effective at different sampling scales to those required to quantify purely floristic differences, but it is difficult to know, without more elaborate investigation, whether one has sampled effectively for both if one is trying to quantify both at the same sampling scale. It is also a much overlooked fact that the scale of disturbance necessarily interacts with the scale of sampling to produce the final ordination pattern, compounding the problem that some ordination patterns may be artefacts of procedure rather than inherent properties of the data in the first instance. Thus, it is also possible that the ordinations reflect not only gradients of change in species composition, but rather, residual floristic makeup in the aftermath of a disturbance regime which has no inherent pattern at all. At the very least, floristic pattern must reflect the historical disturbance regime, the patch-structured nature of the environment, sampling scale, stochasticity and chance. While floristic pattern may be adequately quantified at any one time, the aforementioned factors cannot (see section 11.1.), and nor can the ordinations separate ongoing and historically generated patterns from presently occurring ecological processes.

Despite these uncertainties VB appears consistently different at all structural levels. The floristically distinctive character of VB reflects what is in fact a simple and recent disturbance history. This is because VB was not in fact disturbed, but rather largely destroyed in the 1940s and thus has a recent and relatively simple disturbance history. Subsequent disturbances have occurred against a backdrop of recovery, with its associated hardy and early successional species. The predominance of these hardy generalists in VB has possibly resulted in subsequent disturbances being less noticeable, with recovery from the pool of generalists being rapid.

The general effect of disturbance is further alluded to by the picture presented by the ordinations in three dimensions (submitted as Appendix 1) which both confirm the lack of any consistent separation as well as demonstrating substantial but inconsistent separation on the third axis. The fact that substantial, and inconsistent separation occurs on all three axes suggests the varied and unpatterned response of vegetation to disturbance and the difficulty of gleaning biologically interpretable information from the ordination procedure alone.

8.7. Species lists

8.7.1. Species recorded for Pigeon Valley

CANOPY SPECIES.

Albizia adianthifolia
Bridelia micrantha
Chaetacme aristata
Commiphora woodii
Cussonia sphaerocephala
Scolopia zeyheri

Baphia racemosa
Celtis mildbraedii
Chrysophyllum viridifolium
Croton sylvaticus
Rhus chirindensis
Strychnos madagascariensis

CLIMBERS.

Dioscorea cotinifolia
Flagellaria guineensis
Pyrenacantha scandens
Rhoicissus spp.
Secamone alpinii
Secamone gerrardii

Dioscorea dregeana
Grewia caffra
Rhoicissus rhomboidea
Rhus tomentosa
Secamone filiformis
Secamone spp.

CLIMBER/TREES.

Dalbergia armata

Dalbergia obovata

EMERGENT SPECIES.

Cussonia sphaerocephala

Strychnos madagascariensis

GEOPHYTES.

Drimiopsis maculata

GRASSES.

Digitaria diversinervis
Setaria megaphylla

Oplismenus hirtellis

HERBS.

Cissus fragilis
Commelina erecta
Cyperus albostriatus
Glycine wightii
Secamone gerrardii
Tragus spp.

Coleotrype natalensis
Crocasmia aurea
Cyphostemma hypoleucum
Ipomoea spp.
Sida cordifolia
Vernonia angulifolia

SAPLING SPECIES.

Baphia racemosa
Brachylaena spp.
Canthium obovatum
Celtis africana
Clerodendrum glabrum
Cryptocarya woodii

Bequaerti dendron natalense
Canthium inerme
Canthium spinosum
Celtis mildbraedii
Combretum krausii
Cussonia spp.

Deinbollia oblongifolia
Dombeya tiliacea
Euclea natalensis
Litsea sebifera
Maytenus peduncularis
Mimusops obovata
Oxyanthus pyriformis
Pavetta lanceolata
Rawsonia lucida
Rothmania globosa
Trichilia dregeana
Uvaria caffra

SCRAMBLERS.

Capparis brassii

SEEDLING SPECIES.

Baphia racemosa
Canthium spinosum
Celtis mildbraedii
Cryptocarya woodii
Deinbollia oblongifolia
Isoglossa woodii
Maerua racemulosa
Pavetta lanceolata
Rawsonia lucida
Rothmania globosa
Secamone gerrardii
Uvaria caffra

SHRUBS.

Entada spicata
Monanthotaxis caffra

SHRUB/HERBS.

Vernonia angulifolia

UNDERSTOREY SPECIES.

Albizia adianthifolia
Baphia racemosa
Brachylaena uniflora
Canthium inerme
Canthium spinosum
Celtis mildbraedii
Clerodendrum glabrum
Commiphora woodii
Cryptocarya woodii
Deinbollia oblongifolia
Dovyalis rhamnoides
Lagynias lasiantha
Maytenus peduncularis

Diospyros villosa
Embelia ruminata
Lagynias lasiantha
Maerua racemulosa
Millettia grandis
Ochna natalitia
Pavetta inandensis
Psychotria capensis
Rhus spp.
Strychnos madagascariensis
Tricalysia lanceolata
Xylothea kraussiana

Tylosema spp.

Bequaertiodendron natalense
Carissa bispinosa
Chrysophyllum viridifolium
Dalbergia armata
Flagellaria guineensis
Lagynias lasiantha
Oxyanthus pyriformis
Psychotria capensis
Rhoicissus spp.
Secamone alpinii
Strychnos madagascariensis
Xylothea kraussiana

Jasminum streptopus

Anastrabe integerrima
Bequaertiodendron natalense
Canthium ciliatum
Canthium obovatum
Celtis africana
Chaetacme aristata
Combretum kraussii
Croton sylvaticus
Cussonia sphaerocephala
Dombeya tiliacea
Grewia occidentalis
Maerua racemulosa
Mimusops obovata

Oxyanthus pyriformis
Putterlickia verrucosa
Rhus chirindensis
Strychnos madagascariensis
Tricalysia lanceolata
Vangueria esculenta

Psychotria capensis
Rawsonia lucida
Rothmania globosa
Trichilia dregeana
Uvaria caffra
Xylothea kraussiana

UNDERSHRUB.

Pupalia atropurpurea

8.7.2. Species recorded for Virginia Bush

CANOPY SPECIES.

Albizia adianthifolia
Brachylaena spp.
Melia azedarach
Trema orientalis

Antidesma venosum
Bridelia micrantha
Syzygium cuminii

CLIMBERS.

Cardiospermum grandiflorum

Pyrenacantha scandens

CLIMBER/TREE.

Dalbergia obovata

FERNS.

Cheilanthes viridus

GEOPHYTES.

Drimiopsis maculata

GRASSES.

Digitaria diversinervis
Panicum spp.

Oplismenis hirtellis
Setaria megaphylla

HERBS.

Aneilema aequinoctiale
Cyperus albostriatus
Cyphostemma hypoleucum
Hewittia biloba
Oxalis corniculata
Vernonia angulifolia

Commelina erecta
Cyperus spp.
Desmodium incanum
Ipomoea spp.
Protasparagus densiflorus

EXOTIC HERBS.

Livistonia rhinensis

Suberosa passiflora

SAPLING SPECIES.

Acokanthera oblongifolia
Allophyllus natalensis
Apodytes dimidiata
Bridelia micrantha
Canthium inerme
Canthium spinosum
Carissa bispinosa
Croton sylaticus
Embelia ruminata
Erythrina spp.

Albizia adianthifolia
Antidesma venosum
Brachylaena discolor
Calpurnea aurea
Canthium obovatum
Canthium spp.
Clerodendrum glabrum
Deinbollia oblongifolia
Erythrina lysistemon
Eugenia capensis

Eugenia uniflora
Harpephyllum caffrum
Maytenus procumbens
Morus alba
Psydrax obovata
Rhus chirindensis
Rhus pentheri
Schinus terebinthifolius
Strelitzia nicolai
Syzygium cuminii
Trichilia dregeana
Uclea natalensis

Ficus natalensis
Litsea sebifera
Melia azedarach
Pavetta lanceolata
Psychotria capensis
Rhus nebulosa
Sapium integerrimum
Scutia myrtina
Syzygium cordatum
Trema orientalis
Tricalysia sonderana
Vangueria infausta

SEEDLING SPECIES.

Albizia adianthifolia
Antidesma venosum
Brachylaena spp.
Canthium inerme
Canthium spp.
Coddia rudis
Croton sylvaticus
Erythrina lysistemon
Fagara capensis
Maytenus procumbens
Psydrax obovata
Psychotria capensis
Schinus terebinthifolius
Syzygium cordatum

Allophyllus natalensis
Apodytes dimidiata
Bridelia micrantha
Canthium spinosum
Clerodendrum glabrum
Cordia caffra
Deinbollia oblongifolia
Eugenia capensis
Litsea sebifera
Pavetta lanceolata
Psychotria capensis
Sapium integerrimum
Scutia myrtina
Euclea natalensis

SHRUBS.

Embelia ruminata
Smilax kraussiana

Hibiscus curatensis

UNDERSTOREY SPECIES.

Albizia adianthifolia
Apodytes dimidiata
Bridelia micrantha
Canthium spinosum
Carissa bispinosa
Erythrina spp.
Ficus natalensis
Grewia spp.
Litsea sebifera
Mimusops obovata
Psychotria capensis
Scutia myrtina
Syzygium cordatum
Trema orientalis
Euclea natalensis

Antidesma venosum
Brachylaena discolor
Canthium inerme
Canthium spp.
Clerodendrum glabrum
Eugenia capensis
Grewia occidentalis
Lagynias lasiantha
Mimusops caffra
Psydrax obovata
Sapium integerrimum
Strelitzia nicolai
Syzygium cuminii
Tricalysia sonderana

UNDERSHRUBS.

Abrus precatorius

Isoglossa woodii

Pupalia atropurpurea

Solanum mauritianum

WEEDS.

Chromolaena odorata

Lantana camara

8.7.3. Species recorded for Silverglen Nature Reserve

CANOPY SPECIES.

Anastrabe integerrima
Baphia racemosa
Cryptocarya woodii
Ficus sur
Psyrax obovata
Schotia spp.
Teclea gerrardii

Apodytes dimidiata
Chaetacme aristata
Cussonia nicholsonii
Protorhus longifolia
Rhus chirindensis
Scolopia zeyheri

CLIMBERS.

Behnia reticulata
Dioscorea sylvatica
Pyrenacantha scandens
Rhoicissus tridentata

Dioscorea cotinifolia
Flagellaria guineensis
Rhoicissus tomentosa

CLIMBER/TREES.

Dalbergia armata

Dalbergia obovata

EMERGENT SPECIES.

Catha spp.
Protorhus longifolia

Maytenus peduncularis
Rhus chirindensis

GRASSES.

Setaria megaphylla

HERBS.

Cyperus albostriatus
Dietes vegeta
Ipomoea spp.
Protasparagus falcatus
Tragus durbanensis

Cyphostemma hypoleucum
Drimiopsis maculata
Myrsine spp.
Senecio tamoides

PALMS.

Phoenix reclinata

SAPLING SPECIES.

Acridocarpus natalitius
Baphia racemosa
Brachylaena spp.
Canthium spinosum
Canthium suberosum
Chrysophyllum viridifolium
Clerodendrum glabrum
Combretum kraussii
Commiphora harveyi

Apodytes dimidiata
Bequaertiodendron natalense
Canthium inerme
Canthium spp.
Carissa bispinosa
Clausena anisata
Coddia rudis
Combretum molle
Commiphora spp.

Croton sylvaticus
Cussonia nicholsonii
Diospyros whyteana
Drypetes arguta
Ekebergia capensis
Euclea natalensis
Grewia lasiocarpa
Hippobromus pauciflorus
Lagynias lasiantha
Manilkara discolor
Maytenus peduncularis
Maytenus senegalensis
Pavetta bowkeri
Psydrax obovata
Rinorea angustifolia
Sapium integerrimum
Teclea gerrardii
Turraea floribunda
Uclea natalensis
Vepris lanceolata

Cryptocarya woodii
Deinbollia oblongifolia
Dovyalis rhamnoides
Drypetes spp.
Erythrococca berberidea
Fagara capensis
Grewia occidentalis
Hyperacanthus amenus
Maerau racemulosa
Maytenus mossambicensis
Maytenus procumbens
Mimusops obovata
Protorhus longifolia
Psychotria capensis
Rothmania globosa
Scutia myrtina
Tricalysia lanceolata
Turraea obtusifolia
Uvaria caffra
Xylothea kraussiana

SEEDLINGS.

Albizia adianthifolia
Baphia racemosa
Canthium inerme
Canthium spp.
Celtis africana
Clausena anisata
Combretum kraussii
Cryptocarya woodii
Drypetes arguta
Euclea natalensis
Hippobromus pauciflorus
Lagynias lasiantha
Maytenus peduncularis
Pavetta bowkeri
Pavetta spp.
Rothmania globosa
Euclea natalensis
Vepris lanceolata

Anastrabe integerrima
Bequaertiodendron natalense
Canthium spinosum
Canthium suberosum
Chrysophyllum viridifolium
Clerodendrum glabrum
Commiphora harveyi
Deinbollia oblongifolia
Drypetes spp.
Ficus lutea
Hyperacanthus amenus
Maerua racemulosa
Maytenus procumbens
Pavetta lanceolata
Psychotria capensis
Tricalysia lanceolata
Uvaria caffra
Xylothea kraussiana

SHRUBS.

Cassine velutinum
Entada spicata
Monanthotaxis caffra
Salacia gerrardii

Embelia ruminata
Jasminum streptopus
Passiflora suberosa

UNDERSTOREY SPECIES.

Acalypha glabrata
Baphia racemosa
Berberidea erythrococca
Brachylaena spp.
Canthium spp.

Anastrabe integerrima
Bequaertiodendron natalense
Bersama lucens
Canthium inerme
Canthium spinosum

Chaetacme aristata
Clerodendrum glabrum
Combretum kraussii
Commiphora harveyi
Croton sylvaticus
Cussonia nicholsonii
Diospyros whyteana
Drypetes arguta
Duranta repens
Grewia occidentalis
Hyperacanthus amenus
Lagynias lasiantha
Maytenus spp.
Olea woodiana
Protorhus longifolia
Psychotria capensis
Rhus chirindensis
Sapium integerrimum
Sideroxylon inerme
Strychnos madagascariensis
Teclea gerrardii
Tricalysia lanceolata
Turraea floribunda
Euclea natalensis
Vangueria esculenta
Xylothea kraussiana

UNDERSHRUBS.

Dalechampia capensis
Isoglossa woodii

WEEDS.

Chromolaena odorata

Clausena anisata
Coddia rudis
Combretum molle
Commiphora spp.
Cryptocarya woodii
Cussonia spp.
Dombeya tiliacea
Drypetes spp.
Erythrina lysistemon
Hippobromus pauciflorus
Kraussia floribunda
Maytenus peduncularis
Mimusops obovata
Pavetta lanceolata
Psydrax obovata
Putterlickia pyracantha
Rothmania globosa
Sida cordifolia
Strelitzia nicolai
Strychnos usambarensis
Tecomaria capensis
Trimeria grandifolia
Turraea obtusifolia
Uvaria caffra
Vepris lanceolata

Indigofera micrantha
Monanthotaxis caffra

Lantana camara

8.7.4. Species recorded for Burman Bush

Acalypha sonderana
Albizia adianthifolia
Brachylaena discolor
Chaetacme aristata
Cussonia suluensis
Olea woodiana
Sapium integerrimum
Strychnos decussata
Teclea gerrardii

Acridocarpus natalitius
Baphia racemosa
Celtis africana
Cussonia nicholsonii
Maytenus heterophylla
Rothmania globosa
Sclerocarya birrea
Strychnos madagascariensis
Xylothea kraussiana

CLIMBERS.

Flagellaria guineensis
Pyrenacantha scandens
Rhoicissus spp.
Secamone gerrardii

Grewia caffra
Rhoicissus rhomboidea
Rhoicissus tomentosa

CLIMBER/TREE.

Dalbergia armata

Dalbergia obovata

EMERGENT SPECIES.

Cordia caffra
Strychnos decussata
Xylothea kraussiana

Sapium integerrimum
Strychnos madagascariensis

GRASSES.

Digitaria diversinervis
Panicum laticomum

Oplismenus hirtellus

HERBS.

Abutilon sonneratianum
Coleotrype natalensis
Cyathula psilotrichum
Cyphostemma hypoleucum
Peristrophe cernua
Pupalea atropurpurea
Thunbergia dregeana

Anomatheca laxa
Commelina erecta
Cyperus albostriatus
Diets vegeta
Protasparagus plumosus
Scadoxus spp.

PARASITES.

Erianthemum dregei

SAPLING SPECIES.

Acalypha glabrata
Allophylus melanocarpus
Brachylaena discolor
Carissa bispinosa

Acokanthera oblongifolia
Baphia racemosa
Canthium inerme
Celtis africana

Chaetacme aristata
Combretum kraussii
Croton sylvaticus
Dombeya tiliacea
Drypetes natalensis
Hyperacanthus amenus
Maerua racemulosa
Mimusops obovata
Psydrax obovata
Rapanea melanophloeos
Strychnos decussata
Strychnos usambarensis
Tecomaria capensis
Uvaria caffra

Clausena anisata
Commiphora harveyi
Deinbollia oblongifolia
Drypetes arguta
Euclea natalensis
Lagynias lasiantha
Maytenus heterophylla
Olea woodiana
Putterlickia pyracantha
Rothmania globosa
Strychnos madagascariensis
Teclea gerrardii
Tricalysia lanceolata
Xylothea kraussiana

SCRAMBLERS.

Capparis brassii
Putterlickia pyracantha

Capparis fascicularis
Pyrenacantha scandens

SEEDLING SPECIES.

Acokanthera oblongifolia
Baphia racemosa
Canthium locuples
Chaetacme aristata
Deinbollia oblongifolia
Drypetes natalensis
Maerua caffra
Mimusops obovata
Olea woodiana
Psychotria capensis
Rhoicissus tomentosa
Strychnos madagascariensis
Uvaria caffra

Albizia adianthifolia
Bequaertiodendron natalense
Carissa bispinosa
Clausena anisata
Drypetes arguta
Lagynias lasiantha
Maerua racemulosa
Ochna natalitia
Protorhus longifolia
Putterlickia pyracantha
Rothmania globosa
Teclea gerrardii
Xylothea kraussiana

SHRUBS.

Clerodendrum myricoides
Hibiscus calyphyllus
Monanthes caffra

Entada spicata
Jasminum streptopus
Triumfetta spp.

TREE/SCRAMBLER.

Grewia caffra

UNDERSTOREY SPECIES.

Acalypha glabrata
Allophylus melanocarpus
Baphia racemosa
Canthium spinosum
Coddia rudis
Commiphora harveyi
Cordia caffra
Cussonia sphaerocephala

Acokanthera oblongifolia
Apodytes dimidiata
Brachylaena discolor
Chaetacme aristata
Combretum kraussii
Commiphora spp.
Cussonia nicholsonii
Cussonia zuluensis

Deinbollia oblongifolia
Dombeya tiliacea
Drypetes spp.
Euclea natalensis
Hippobromus pauciflorus
Lagynias lasiantha
Mimusops obovata
Psydrax obovata
Rothmania globosa
Strychnos madagascariensis
Tricalysia lanceolata
Xylothea kraussiana

Diospyros natalensis
Drypetes arguta
Ehretia rigida
Grewia occidentalis
Kraussia floribunda
Maerua racemulosa
Olea woodiana
Putterlickia pyracantha
Strychnos decussata
Teclea gerrardii
Turraea floribunda

UNDERSHRUBS.

Abrus precatorius
Osyridicarpos schimperianus

Isoglossa woodii

WEEDS.

Chromolaena odorata

XEROPHYTES.

Sansevieria guineensis

Sansevieria hyacinthoides

8.7.5. Species recorded for Stainbank Nature Reserve

CANOPY SPECIES.

Anastrabe integerrima
Bequaertiodendron natalense
Cassipourea gummiflua
Combretum molle
Hyperacanthus amenus
Millettia grandis
Ptaeroxylon obliquum
Teclea gerrardii
Vepris lanceolata

Baphia racemosa
Brachylaena spp.
Chaetacme aristata
Croton sylvaticus
Maytenus peduncularis
Oricia bachmannii
Strychnos madagascariensis
Turraea floribunda
Xylothea kraussiana

CLIMBERS.

Diospyros sylvaticus
Pyrenacantha scandens
Secamone alpinii

Flagellaria guineensis
Rhoicissus rhomboidea
Secamone gerrardii

CLIMBER/TREES.

Acacia kraussiana
Dalbergia obovata

Dalbergia armata

EMERGENT SPECIES.

Brachylaena spp.
Celtis africana
Ficus sur
Millettia grandis
Protorhus longifolia

Calodendrum capense
Cussonia spp.
Maytenus peduncularis
Olea woodiana

FERNS.

Pelaea viridus

GRASSES.

Oplismenus hirtellus

Panicum spp.

HERBS.

Cissus fragilis
Cyperus albostriatus
Dietes vegeta
Protasparagus falcatus
Protasparagus tomentosa

Coccinia palmata
Cyphostemma hypoleucum
Dracaena hookeriana
Protasparagus plumosus

SAPLING SPECIES.

Baphia racemosa
Drypetes spp.

Bequaertiodendron natalense
Hyperacanthus amenus

Millettia grandis
Oricia bachmannii
Peddiea africana
Rhus chirindensis
Strychnos usambarensis
Euclea natalensis
Vitellariopsis marginata

Mimusops obovata
Pavetta bowkeri
Rawsonia lucida
Rothmania globosa
Tricalysia lanceolata
Uvaria caffra

SCRAMBLERS.

Capparis brassii

Capparis tomentosa

SEEDLING SPECIES.

Baphia racemosa
Calodendrum capense
Clausena anisata
Euclea natalensis
Kraussia floribunda
Olea woodiana
Pavetta bowkeri
Ptaeroxylon obliquum
Rhus chirindensis
Strelitzia nicolai
Teclea gerrardii
Uvaria caffra
Xylothea kraussiana

Bequaertiodendron natalense
Canthium spinosum
Drypetes spp.
Hyperacanthus amenus
Maytenus mossambicensis
Oricia bachmannii
Peddiea africana
Rawsonia lucida
Rothmania globosa
Strychnos usambarensis
Tricalysia lanceolata
Vitellariopsis marginata

SHRUBS.

Monanthotaxis caffra

UNDERSTOREY SPECIES.

Acokanthera oppositifolia
Baphia racemosa
Brachylaena discolor
Canthium spinosum
Cassipourea gerrardii
Coddia rudis
Combretum molle
Cussonia spp.
Drypetes spp.
Hippobromus pauciflorus
Maerua caffra
Oricia bachmannii
Psychotria capensis
Rawsonia lucida
Scolopia zeyheri
Teclea gerrardii
Uvaria caffra
Wrightia natalensis

Anastrabe integerrima
Bequaertiodendron natalense
Canthium inerme
Carissa bispinosa
Chaetacme aristata
Combretum kraussii
Croton sylvaticus
Dracaena hookeriana
Euclea natalensis
Hyperacanthus amenus
Millettia grandis
Pavetta lanceolata
Ptaeroxylon obliquum
Rothmania globosa
Strychnos usambarensis
Tricalysia lanceolata
Vitellariopsis marginata
Xylothea kraussiana

UNDERSHRUBS.

Isoglossa woodii

WEEDS.*Chromolaena odorata**Datura spp.*

PART TWO.

9. A pause, to reflect

"The proliferation of competing articulations, the willingness to try anything, the expression of explicit discontent, the recourse to philosophy and to debate over fundamentals, all these are symptoms of a transition from normal to extraordinary research"

--/- Thoman Kuhn, 1970 ---

The aims of this thesis as stated in points 1, 2 and 3 of the introduction have not been satisfactorily accomplished and the next step is to ask why. This raises questions about the appropriateness of methods used, the availability, or lack thereof, of more suitable methods, and the assumptions underlying those methods currently in vogue. If the inconclusiveness of the results suggest weaknesses in the current paradigm, then it will be useful to consider what these weaknesses may be, and what can be done about it.

In the spirit of the introduction to this thesis, it is these subjects which I now propose to investigate.

Sections 10. and 10.1. refer the reader to some of the challenges inherent in attempting even to theorise about the problems encountered in sections 7. and 8.. While theory is shown to have its place, a consideration of theory leads the reader to reflect on some fundamentals such as the value of hypothesis testing, the need for descriptive study that is not theory-laden, problems of scale, pattern and heterogeneity and some challenges inherent in systems theory thinking as opposed to reductionism. In more specific vein, section 11. suggests difficulties that arise through lack of systematization, and the differences in approach, interpretation and method that characterize this field. Also, the notion of conditioning by paradigm is raised, as are the difficulties in creating a unifying paradigm in the face of a confusing diversity of approaches. Section 11.1. describes the difficulty of defining the role of ecology in this field, confusion regarding the nature, operation and type of processes ecologists and biogeographers deal with, difficulties of scale and the need to question our constructions and categories. These theoretical and philosophical problems are given a brief, but necessary context in section 12. which provides an overview of the demographic, socioeconomic and ecological problems and opportunities that arise in the urban context. Section 12.1. argues that the ecological study of the effects of urbanisation has the potential to constitute a necessary and radical expansion of ecology to include aesthetics, recreation, religion and

psychology, the latter two concerns having relevance to the conclusion of this thesis in section 23..

Sections 13., 14. and 15.1. contain guidance for the reader as to their relevance, in setting the scene for further recourse to philosophy in section 15.2..

10. The role and necessity of theory

"Oversimplified caricatures of reality
nevertheless have a use, if only in posing
questions and sharpening discussion"
(May, 1976)

"The answer is 'yes' or 'no' depending
on the interpretation"
Albert Einstein, quoted in
Scientific American, April, 1950

It is interesting to note that the value of theory itself is not beyond question. Whiteman (1967) makes a distinction between theory and what he terms a 'commonsense' view to denote an 'intuitive grasp' of "what is so" that renounces all dependence on theories. Whiteman explains this 'intuitive grasp' as the kind of "comprehension that arises when the total state of affairs, as it meets us face to face, is held in mind objectively in that form, without addition of thought or imagination". Whiteman concedes however, that the "provisional trying out of theories" is often required, given the difficulty of cultivating the power of intuitive analysis.

In doing justice to one's conceptualisation of the problem with which this thesis is concerned, it should be placed within the elaborate body of, in this case, ecological and biogeographical theory. While management and conservation concerns demand emphasis on practical application and workability, it is arguable whether problem-orientated or policy-directed research can afford to ignore theory at any level if it is to be meaningful in the long term. The need to successfully integrate biogeographic and ecological theory (and even taxonomy) with practical attempts to manage and conserve species in urban areas has been suggested by Poynton (1985) and Poynton and Roberts (1985a;1985b). As Tilman (1989) states, "Even the most ardent empiricist is, of necessity, a theoretician, for it is impossible to measure everything in an ecosystem". Unfortunately, it is difficult, too, to keep abreast of all ecological theory.

Although theory dealing with the properties of communities is not well established, theory, both mathematical and nonmathematical, can be useful even where it can only provide general understanding of a system without allowing very accurate

predictions to be made (Ehrlich, 1989). In conservation biology, for example, this has proven to be the case in the notion of "minimum viable population". The mathematical concept is rooted in population genetics and demographic theory. Although the theory does not allow for specific survival predictions within specific time frames (in part because it requires more thorough empirical data than are normally available) it does prompt managers to be alert to situations in which there is a danger of inbreeding depression or stochastic extinction (Ehrlich, 1989). Furthermore, the theory shows promise that with further development its predictive value can be greatly increased.

The theory that has attracted most attention in the rapidly developing area of conservation biology is the Equilibrium Theory of Island Biogeography, which has stimulated a great deal of empirical research, especially in the study of the effects of fragmentation on biotas. The controversial nature of the theory has generated a substantial literature (Ehrlich, 1989). The principal criticism of the theory (e.g. Simberloff and Abele, 1982) is that it is too simplified a representation of the real world to be useful. Ehrlich (1989) maintains that although the problems recognised by Simberloff and his colleagues are real, they reflect more the failure of many ecologists to understand the uses of theory than an inadequacy in the theory itself. Ehrlich (1989) points out that the applicability of the theory clearly will vary from situation to situation and that the important point, is that in the various controversies, the theory has served two of the main functions of theory - that of providing a coherent basis for discussing complex issues, and transforming the way an entire area of intellectual endeavour was approached. Regarding the relevance of theory to urban-ecological planning in the greater Durban area, such sentiment is confirmed by Roberts, D.C. (1990).

More importantly, some contemporary discussion about the role of theory in ecology reflects a more general discussion about how science should be done. Roughgarden, May and Levin (1989) point out that the writings of Karl Popper, currently much in vogue, may be interpreted as a "denying of legitimacy to research programs not cast in terms of falsifiable hypotheses". These authors maintain however that philosophies of science are themselves theories rather than revealed truths, and contentions that any one of them defines the correct way to do science are abundantly falsified by the actions of practising scientists. There is a special necessity for descriptive study in ecology where much ecological modelling and field-experimentation has been flawed by insufficient descriptive knowledge of the system (Pomeroy, Hargrove and Alberts, 1987). These authors maintain that while descriptive work must be justified in terms of what we need to know for higher scientific purposes, it is unrealistic to believe that descriptive work can always be directly and immediately linked to the needs of testing some specific hypothesis. Mentis (1988a) states with respect to ecology, that "Powerful testing demands focus on only one or a few hypotheses" but that this risks "blinking our science, particularly in a field that espouses greater or lesser interconnectedness and holism".

Scientific orthodoxy in this regard is increasingly being challenged e.g. Poynton (1985), Goodall (1977), Gleick (1987), Pomeroy, Hargrove and Alberts (1987), Mentis (1988a), Peat (1989), Macy (1991).

It is not the intention of this thesis to provide an exhaustive account of possibly relevant ecological theory. Besides being beyond the scope of such a project, the relevance of much ecological theory (much of which has been developed from work in tropical and temperate forest ecosystems) to the extremely small and disturbed forests with which this project is concerned, is difficult to ascertain. An attempt will be made, therefore, to discuss theory briefly where it is thought to be particularly important.

10.1. Structure and function of ecosystems and communities: challenges in the development of theory

"The pattern seen as characteristic of any system is 'neither a property of the system alone nor of the observer, but of an interaction between them'"

Levin, (1987) in Kelly and Harwell, (1990).

The concerns of environmental management require an understanding, at some level, of what the natural patterns and dynamics of ecosystems are, how they are regulated, how robust they are, and how they respond to stress.

Levin (1989) states that the solutions to the environmental problems we face will require an integration of experimental and theoretical approaches at a variety of levels of specialisation, and that no single model, or level of description will suffice, i.e. models will have to range from the generic to the site- and situation-specific. Levin maintains that while generic models are essential in providing the framework within which site-specific studies are set, site-specific studies provide the test cases which make the general theory useful. Levin's contention is that theory without data is sterile, while data without theory are uninterpretable.

Classical views of ecological communities have been dominated by the Clementsian approach which treated the community as an integral unit, a superorganism which was essentially homogeneous and equilibrial in that it tended to a unique, locally defined climax state (Levin, 1989). Mathematical theory was even more orthodox in orientation, and its adherence to the notions of homogeneity and equilibrium, and the concept of the community as a well defined unit, is increasingly being criticised (Levin, 1989).

Increasingly, the community, rather than being viewed as a well defined entity, is a concept of convenience, dynamic in space and time, and reflecting the individualistic properties of its

component species. This view, emphasizing the importance of stochastic phenomena, has been mirrored in the elucidation of the importance of gap phase phenomena in forest dynamics (Levin, 1989).

Thus, ecological communities and ecosystems are seen as being heterogeneous in space and time, and this heterogeneity affects diversity and the evolution of life histories (Levin, 1989). Biotic heterogeneity reflects underlying heterogeneity in the abiotic environment, and the stochastic phenomena associated with disturbance and colonisation. This perspective highlights the need for new approaches that can deal with the irregular, fractal patterns exhibited by fragmented landscapes, and with the fluctuating spatio-temporal mosaics that are characteristic of ecosystems and landscapes (Levin, 1989).

Given such views, it follows that worthwhile characterisation of ecological problems in real landscapes, where equilibrium and its related concepts are not absolutes, will depend critically on the scale and nature of investigation. Furthermore, it is unlikely that there is a single correct scale of investigation, and description of the dynamics of ecosystems must look across scales to examine how system description depends on the scale of investigation (Levin, 1989). This idea may be especially important where, for instance, forest patches under study are highly disturbed and particularly small.

The theoretical importance of an awareness of scale is evident in the extension of the Theory of Island Biogeography to nonequilibrium situations, in which temporary islands form and disappear. Examples of forest gaps e.g. Pickett and Thompson (1978), Pickett and White (1985) provide examples of such situations (Levin, 1989). In such situations disturbance upsets or prevents an 'equilibrium' situation, reinitiating a successional dynamic and providing colonization opportunities for species that would be excluded from more mature successional stages.

In modelling such systems Levin and Payne (in Levin, 1989) focussed attention on the individual patch and on the distinct spatial and temporal scales associated with within-patch versus among-patch events. This leads to an initial development of demographic accounting for the distribution of patches, relating the age and size frequency distribution of patches to descriptors of patch birth, growth and death (Levin, 1989). Complementing this are descriptions for the possible colonization sequence of patches in relation to properties such as size, location and time of formation. Levin points out that although this model was a generic one, its usefulness came from specific applications to particular systems, and from in-depth studies of recolonization and competition in gaps. Such studies have now been carried out for a wide variety of terrestrial and intertidal systems (Pickett and White, 1985 in Levin, 1989).

Although such approaches are a beginning, they leave unresolved the issue of the determination of pattern on a continuum of

scales. Disturbances come in a wide variety of shapes and sizes and these and other events introduce complicated patterns of spatial and temporal correlation (Levin, 1989). Nonetheless, it is being increasingly realised that complex ecological phenomena are best studied through investigation at several hierarchical levels on appropriate spatial and temporal scales (e.g. Pickett, Kolasa, Armesto and Collins, 1989), with attention paid to both lower-level driving processes and higher-level regulating processes (Bazzaz and Sipe, 1987). This kind of thinking is seemingly consistent with that of General Systems Theory, arguably an alternative (Holroyd, 1989) to what Mentis and Siegfried describe as "the growing pile of rubble" scientists in the "Baconian-Newtonian-Cartesian paradigm" have produced, in "patiently describing brick after brick in the hope that in the end the grand edifice will emerge itself" (Mentis and Siegfried, published in the journal *Optima*, date unknown).

Awareness of the importance of scale is increasingly evident in the ecological literature e.g. Regier and Cowell (1972), Bazzaz and Sipe (1987), Pomeroy, Hargrove and Alberts (1987), Urban, O'Neill and Shugart (1987), O'Neill (1989), Kelly and Harwell (1990), Matson and Carpenter (1990), and Hinds (1984) with respect to statistical considerations.

Lastly, it is worth pointing out, that for them to be useful, theories need to develop from being simply conceptual frameworks, to more powerful sources of testable hypotheses (Steele, 1989).

As understanding of the functional processes of indigenous forests (Geldenhuys ed. 1989) is constrained by theory, so are available methodological and theoretical perspectives constrained by paradigm. Thus, consideration of the types, history, and quality of thinking encountered in the ecological and biogeographical disciplines with which this project is concerned, becomes relevant.

11. Methodological and conceptual problems encountered during the project

Few conceptual analyses of the problems facing ecologists working in highly and variously disturbed urban environments have been attempted (but see Roberts, D.C., 1990). It is axiomatic that there are myriad conceptual and methodological problems that are more intractable than they would be in the less disturbed and/or more homogenous environments in which phytosociology has its background.

Recent literature on disturbance ecology (e.g. Pickett and Thompson, 1978; Pickett and White, 1985) has provided ecologists with a confusing range of intuitively pleasing, but generally unhelpful theorisation. Indeed, recent literature (e.g. Poynton, 1986; Myers and Giller, 1988) suggesting confusion in the field of historical biogeography is instructive here to aid diagnosis of similar confusion in the literature in the fields of disturbance ecology and ecological biogeography. The strong geographical component in this study makes a close inspection of biogeographical theory necessary in any case.

According to these authors, this confusion can be attributed primarily to the following:

1. Lack of systematization has resulted in little consistency in the formulation of hypotheses, with the result that these, as well as much biogeographical data, are not comparable. Furthermore, biogeography has suffered from inattention to the formulation of applicable, coherent, and testable hypotheses (Poynton, 1986; Myers and Giller, 1988).

The call to develop theories from mere conceptual frameworks into more powerful sources of hypotheses is not a new one in ecology e.g. Pickett and White (1985), Steele (1989).

2. Differences in interpretation, approach and method have been largely unresolvable on account of the positions of different workers not being demarcated clearly enough (Myers and Giller, 1988), and much misunderstanding has been engendered by confused terminology.

Comparable criticism has been levelled at ecology which treats evolutionary, population, community, ecosystem and landscape ecology as separate subdisciplines, between which there is little communication or synthesis e.g. Whittaker, 1974; Pimm, 1984; Pomeroy, Hargrove and Alberts, 1987. Factors on different levels of organisation - ecosystem, plant community, ecophysiology, whole plant physiology, cell physiology, genetics etc. lack unified protocols for integrated analysis, leading to confusion and logical problems in causal ecosystem analysis (Gigon, 1987). As a result, explanations of pattern are usually consistent only within a particular subdiscipline; seldom across all of them (Tilman, 1989). Criticism of the lack of dialogue between ecological theoreticians and empiricists abounds (Kareiva, 1989), and disturbance ecology has produced a plethora of terms (disturbance, resilience, perturbation, stress) which have been used synonymously, inconsistently and ambiguously (Margalef, 1974; Rykiel, 1985). Often, poorly defined terms reflect an uncertainty about what concepts are useful in ecology, and more importantly, what we wish to understand about natural systems (Orians, 1975).

3. The discipline has progressed along the two divergent avenues of pattern definition (historical biogeography), and process identification (ecological biogeography). While it is incorrect to wholly attribute only pattern to historical biogeography and only process to ecological biogeography, these approaches are nonetheless based on palaeontology and systematics, and ecology, respectively, making for a confusing diversity of approach.

Ecologists, similarly, tend to structure their approaches to the study in different ways. Instead of a set of unifying concepts about the structure and functioning of ecosystems, ecology is confronted with an array of definitions, approaches and interpretations (Schulze and Zwolfe, 1987). The pluralistic approach ecologists adopt in the analysis of ecosystems and their subsystems is elaborated on by Schulze and Zwolfe (1987).

4. Uncritical acceptance of certain paradigms as a 'necessary initial premiss of all biogeographical enquiry' (Ball, 1977 in Poynton, 1986) has resulted in inertia in the science, due to its workers being conditioned by paradigm. Decisions regarding choice of paradigm have received little attention (Poynton, 1986). This situation is no less serious in ecology, see 2. Even subjects such as ecological succession involve confrontation between holism (the view emphasizing unity and integration in nature) and reductionism (Finegan, 1984).

5. The processes with which biogeography is concerned occur over short temporal and small spatial scales (ecological biogeography), as well as over evolutionary and geological time, on a global scale (historical biogeography). Ecological biogeography and Conservation Science make use of theories of resource availability, competition, population dynamics, predator-prey interactions and species-area relations. The new discipline of Conservation Science (Conservation Biology) in turn makes use of Island Biogeographic theory, the SLOSS debate, the use of corridors, concepts of minimum viable populations, genetic factors including effective population sizes, inbreeding depression, drift, bottlenecks and outbreeding depression (Simberloff, 1988). Further considerations in this field include demographic and environmental stochasticity, as well as the stability and resilience of ecosystems. Within each of these compartments a large number of theories, hypotheses and models have been proposed to explain observed phenomena. To a large extent these compartments have been non-interactive, which is understandable, given the variety of different interests and backgrounds of the researchers involved (Myers and Giller, 1988). Thus, even to synthesize all of what is known is a major challenge. It requires ecologists and ecological biogeographers to bring together and interrelate ideas and knowledge concerning mechanisms of ecological interaction and evolutionary change, and the present and past distributions of different taxonomic and ecological groups of organisms (Brown and Gibson, 1983) in a way that allows for many sub-disciplines to be brought into working contact with each other. Brown and Gibson (1983) note the difficulty of creating a unifying paradigm within which to achieve this. Ecology is a science, which like biogeography, "has lacked for most of its history the scrutiny of presuppositions, approaches, aims and methods which characterise a philosophically strong discipline" (Poynton, 1986).

Tilman (1989) points out that the vastness of the ecological literature makes it difficult for anyone's knowledge to bridge its different subdisciplines. He states, however, that major advances are likely to come from those attempting syntheses across subdisciplinary boundaries, for this will allow them to test their hypotheses against the accumulated knowledge of all of ecology and not just that of a single subdiscipline.

As Gleick (1987) maintains, "The rare scholars who are nomads by choice are essential to the intellectual welfare of the settled disciplines."

The implications of such assertions are important in assessing how much we can claim to know, and how sure we can be about claims to methodological superiority of certain approaches over others.

11.1. 'Meaningful reality or perceptual convenience'

"You must not...be too precise or scientific
about birds and trees and flowers..."

--- Whalt Whitman, *Specimen Days* ---

"A long-lived inquiry produces a discriminating
language. The very order of the language, the
ecology of its sounds and thoughts, derives
from the mind's intercourse with the landscape"

---- Barry Lopez, *Arctic Dreams* ----

This consideration recently received overdue attention in a paper by Mentis (1988a) in which he alluded to the partial nature of supposed 'fact' with the assertion: "how we conduct our ecology is no less important than the facts which it produces". Comparable sentiments are instructive here, of Holling (1973) whose claim that "Our traditional view of natural systems might well be less a meaningful reality than a perceptual convenience" demonstrated a remarkable prescience of much subsequent literature e.g. Mentis (1980, 1988b), Mentis and Bailey, (1990), Gleick (1988, 1990), Godfray and Blythe (1990), Sattler (1986). The importance of such sentiment is that it is indicative both of changing views of how we see the functioning of ecosystems, as well as changing paradigms and associated methodological approaches in science.

Symptomatic of this state flux in paradigm, and lack, both of clarity and common procedure (Poynton, 1986), is a seeming lack of consensus or analysis of the role of ecology in the field of biogeography (Poynton, 1986). Given that management requires an understanding of both the ecological and biogeographical dynamics affecting species and habitat diversity, and in particular those processes leading to extinction, this becomes crucial. The role of ecology, however, is difficult to define. Myers and Giller (1988) make the point that when analytical methods are used in biogeography, the patterns obtained from them may be neither wholly historical nor wholly ecological, and considerable refinement, testing and reasoning is needed if the effects of these processes are to be distinguished. In small, fragmented and isolated forests, where patchy distributions, slow growth, various, ubiquitous, and often unknown disturbance histories prevail, such considerations are necessarily important. Myers and Giller (1988) go on to make the point that although most biogeographers see the categories of historical and ecological biogeography as the primary subdivision of the subject, ecology and history are not themselves mutually exclusive, certainly the past is wholly continuous with the present. Again, in disturbed

urban areas where the 'ghost of disturbance past' is ever reflected in the environment, this is particularly relevant. Myers and Giller (1988) point out that environmental processes operate on every spatial scale from microhabitat to global, and that it is only the larger scales that are directly relevant to biogeography. There is no absolute or obvious threshold, however, beyond which ecological factors can also be called geographical. Spatially, therefore, this part of ecological biogeography is effectively an integration of these ecological processes on a geographical scale (Myers and Giller, 1988), although how such a statement is meant to aid the practising scientist is questionable. It does not follow, however, that every ecological factor has a geographical dimension, and extension of ecological processes on a geographical scale may itself be hypothetical (Myers and Giller, 1988).

The decision regarding whether or not this hypotheticality exists is not made any more tractable when Myer and Giller (1988) go on to question whether biogeographic processes *per se* exist at all. They maintain that large scale abiotic processes (tectonic, eustatic, climatic and oceanic) will always operate in concert, and that on a local scale abiotic disturbances such as fire, hurricanes and volcanic eruptions also influence distribution patterns in many types of habitat. The biotic processes occurring in concert with the abiotic, are both evolutionary (adaptation, speciation and extinction) and ecological (predation, competition and dispersal), and these in turn operate in conjunction with each other. Myers and Giller (1988) maintain that dispersal may have a claim to being a truly biogeographical process, although establishment of a population seeded by propagules after a dispersal event is clearly an ecological process.

Despite confusion regarding the nature, operation and type of processes biogeographers are dealing with, explanatory biogeography claims to discover process through the identification of pattern (Myers and Giller, 1988). This calls into question the validity of our interpretation of pattern. Myers and Giller (1988) maintain that too little knowledge of process probably leads to an overloading of assumptions, and that this makes it particularly dangerous when invoked processes are assumed from the outset, and all observations follow on narratives which are based on these assumptions. Myers and Giller maintain that what biogeographers often see are patterns arising from short term ecological processes. They maintain that for any particular geological horizon, including the present, these demonstrate (or appear to demonstrate) short-term changes in the distribution of organisms, or relate (or appear to relate) such changes to short-term causal mechanisms, principally ecological factors. The historical propensity of western science to circumscribe causality with both superficial terminology and limited insight (Steinbeck, 1958; Capra, 1982; Wolf, 1985; Weber, 1986; Gleick, 1988; Holroyd, 1989; Sheldrake, 1990; Macy, 1991; Peat, 1991) is notable here. This scenario is complicated by the fact that change takes place over a whole hierarchy of time scales, and that causes and effects of short-term changes differ fundamentally from those taking tens or hundreds of millions of

years. This multiplicity of spatial and temporal scale makes it difficult for the precise operation of processes fundamental to biogeographic understanding to be elucidated. The question of using observed patterns in organism distribution to infer process has been considered by Rosen (in Myers and Giller, 1988) who considers that some of the problems in biogeography have probably arisen from misunderstandings about the perceptual or hypothetical nature of patterns. Rosen claims that if the kind of patterns that scientists derive from their data are formalised perceptions (and therefore subjective), then the observations, results and conclusions drawn from them do not exist in an objective vacuum. According to Rosen, patterns are representational; "they are distinct from the truth, which in many cases might be unknowable". With respect to pattern, Brown and Gibson (1983) state that one of the major problems in biogeography is to distinguish patterns from randomness, and to understand how stochastic processes and deterministic biological mechanisms interact to influence the diversity, distribution and abundance of organisms. The problem is complicated by the fact that most biological and physical processes are neither completely stochastic nor entirely deterministic. The degree of apparent randomness is often largely a matter of spatial or temporal scale.

In assessing the relevance of, and providing added context for the above, a consideration of the central questions and interests of ecological biogeographers is necessary.

12. The problem's urban context

"on ITV and BBC they talk about the curse
philosophy is useless, theology is worse
history boils over, there's an economics freeze,
sociologists invent words that mean 'Industrial Disease'"

-- Mark Knopfler --

The importance of conserving plant communities in urban areas has been clarified by Roberts, D.C. (1990) and will not be reiterated here.

The 20th century has seen an unprecedented flood of people moving from rural to urban areas, with the rate of urbanisation in Africa being the highest in the world (Huntley, Siegfried and Sunter, 1989). Huntley *et al.* (1989) maintain that at an increasing rate of 5.1 % per annum, urban populations in Africa will double every fourteen years. In South Africa the urban population is expected to grow from 16.2 million in 1985 to 35.7 million by the year 2000, by which time 79 % of Africa's population will be urbanised (Huntley *et al.* 1989). These

authors maintain that by the year 2010 the Pretoria-Witwatersrand-Vereeniging area could be one of the 20 largest megacities in the world.

It is realistic to assume that the urbanisation of blacks - an addition of 750 000 to the urban population by the end of the century, will focus principally on the four major metropolitan areas (P.W.V., Cape Town, Durban-Pietermaritzburg and Port Elizabeth-Uitenhage) resulting in an increase in the absolute number of urban blacks from 7.7 million in 1980 to 26 million by 2000 (Davies, 1985).

The urbanisation process will place huge demands on resources such as land, water, housing, urban infrastructure and skilled manpower. In 1985 the shortfall for black housing units was between 550 000 and 850 000, and some two to three million new dwelling units are needed by the turn of the century, equivalent to the construction of 1000 units per working day up to the year 2000 (Huntley *et al.* 1989). 75 % of blacks are unable to afford homes without some form of subsidy and one in every five are without a legal home; more blacks live illegally in Umlazi than whites in Natal (Huntley *et al.* 1989).

Including commuters, Durban's population is presently estimated as being in the region of 3 million people (a number expected by Huntley *et al.* (1989) to double by the end of the century), most of whom live in marginalised economic conditions in squatter settlements both within and on the urban periphery. The growth of such settlements is unparalleled in South Africa's history, and those that surround Durban are said to parallel Mexico City in terms of the rate of their expansion through the 1980's (Huntley *et al.* 1989). It is widely held that Durban is the second fastest growing city in the world (Botha, 1988 in Roberts *et al.* 1989). One can reasonably assume that increasing disturbance in remaining natural areas in Durban is portended by such figures.

Davies (1985) concludes his paper, "When ! - Reform and Change in the South African City", with the hope that it will have suggested the extraordinary complexity that will face the city of the future, and will have identified the "rich wealth of theoretical enquiry, empirical research needs and imaginative conceptualisation that will be necessary to establish the bases of a new urbanism". A similar emphasis on theoretical enquiry, empirical research, and accurate conceptualisation of the problem, as well as recognition of its dynamic nature and inherent complexity, is necessary in considering the implications that city growth has for urban conservation and the protection of natural areas within the city.

12.1. The use of urban gradients in ecological studies

Viewing urbanisation as a massive unplanned experiment, McDonnell and Pickett (1990) suggest that one could use the term "urbanisation" as a convenient shorthand for the ecological forcing functions created by the growth of cities and associated

human activities. These authors state that the individual components (e.g. structures, physical and chemical environments, populations, communities, ecosystems and human culture) must be quantified, and correlations among them assessed, to discover the ecologically important impacts of urban development and change. This picture is further broadened by the contention of Burgess and Sharpe (1981) that the issues of landscape management are not solely ecological, but encompass social, ethical, economic and demographic considerations as well. These authors contend that in any drive for preservation in the face of competing demands, value judgements must incorporate ecology, along with aesthetics, recreation, religion and psychology. These authors argue that ecologists have to participate in the complex process of identifying issues and then finding ways to infuse the results of multivariate analyses into environmental planning and resource decision making. Burgess and Sharpe's opinions in this respect are locally affirmed by Roberts, D.C. (1991) who has discussed extensively the importance of such issues.

McDonnell and Pickett (1990) state that the ecological study of the effects of urbanisation can focus either on metropolitan areas as wholes or on natural areas within metropolitan areas, but that in any event the study of the metropolis as an ecosystem, including its human inhabitants and institutions, would be a radical expansion of ecology. These authors suggest that urbanisation should be exploited as a research subject in ecology, and maintain that the effects of urbanisation can provide a context for answering ecological questions of general importance and applicability, as well as questions that are specific and unique to urbanisation. Given the increasing need to integrate human-modified landscapes with more natural biological communities, and to restore degraded ecosystems in order to minimise human pressures on remaining natural ecosystems (Soule and Kohm ed., 1989) the relevance of urbanisation to the overall topic of disturbance is obvious.

McDonnell and Pickett (1990) invoke the gradient paradigm in ecology (Whittaker, 1967; Austin, 1987; Stevens, 1989 in McDonnell and Pickett, 1990) as an organising tool for ecological research on urban influences on ecosystems. They maintain that the gradient paradigm provides a useful basis for ecological studies of the spatially varying effects of urbanisation (Ter Braak and Prentice, 1988 in McDonnell and Pickett, 1990) on the basis of the fact that urban areas appear so often as dense highly developed cores, surrounded by irregular rings of diminishing development (Dickinson, 1966 in McDonnell and Pickett, 1990). They contend that, like natural environmental gradients, urbanisation should present ecologists with a rich spatial array to use in explaining or predicting environmental and ecological effects. These authors contend, moreover, that urban-rural gradients provide an opportunity to explicitly examine the role of humans.

In questioning why studies of ecological systems along urban-rural gradients should be undertaken, McDonnell and Pickett (1990) point out that from an ecologist's perspective urbanisation produces a variety of unprecedented and intense experimental manipulations. Examples of these include changes in:

1. disturbance regimes
2. biota
3. landscape structure
4. physiological stresses e.g. air pollution
5. cultural, economic and political factors

In most cases, both the spatial extent and magnitude of the manipulations are greater than ecologists are typically able to produce (McDonnell and Pickett, 1990). Furthermore, the coarse-scale, anthropogenic manipulations of ecological systems along urban-rural gradients provide an opportunity to address basic questions at various spatial scales. For example, questions related to hierarchy theory could be addressed, as well as those affecting the scale at which ecological processes and patterns uniquely appear (O'Neill, DeAngelis, Waide and Allen, 1986 in McDonnell and Pickett, 1990). Hierarchy theory is important as a consideration in questions relating to minimum dynamic area (Pickett and Thompson, 1978), the determination of which needs to be based on knowledge of disturbance-generated patch size, frequency and mobility (Pickett and Thompson, 1978).

Questions falling within the general framework of disturbance theory could also be examined. In disturbance theory, manipulations of disturbance regimes may be used to determine the significance of disturbance types, intensities and frequencies in communities and ecosystems (Pickett and White, 1985 in McDonnell and Pickett, 1990). The study of the interactions between urbanisation and disturbance regimes and their effects on ecological processes provide opportunities to advance understanding in this general area (McDonnell and Pickett, 1990), and this is a concern of the present thesis.

At a conceptual level McDonnell and Pickett (1990) argue finally that the intimate involvement of humans with the urban-rural gradient suggests that it would be an unparalleled situation in which to integrate humans as subjects for ecological study, human ecology being the discipline enquiring into the patterns and processes of interactions of humans with their environments (Boyden, 1977; Boyden and Millar, 1978 and Vayda, 1983 in McDonnell and Pickett, 1990). Human values, wealth, life styles, resource use and waste etc. must affect and be affected by physical and biotic environments. The nature of these interactions is a legitimate ecological research topic and one of increasing importance (McDonnell and Pickett, 1990).

In discussing specific uses of urban-rural gradient studies (based in part on a study of ecosystems in the New York City Metropolitan area) McDonnell and Pickett (1990) make mention of remnant forest patches still existent in the city, as well as elsewhere on the land-use gradient, as providing an excellent opportunity to investigate long-term human impacts on forest ecosystems.

Some of their findings, as well as the questions these have raised, are briefly described here, as an example of how relevant

questions can be arrived at through the pursuit of ecological studies in urban areas.

12.1.1. Soil resources : A preliminary study of the physical and chemical properties of forest soils along an urban-rural land use gradient revealed that the soils at the urban end of the gradient were more hydrophobic than rural sites (White and McDonell, 1988 *unpublished manuscript* in McDonell and Pickett, 1990). This novel pattern provides a stimulus to address several ecological questions, including the following:

1. Is the formation of the hydrophobic soil the result of natural processes or new anthropogenically derived sources?
2. How does the pattern of hydrophobicity vary in time and space?
3. Does it limit resource availability to plants (e.g. by reducing N mineralization)?
4. How does it affect litter decomposition rates and below ground processes?
5. Does it affect soil to atmosphere gas fluxes?
6. Is it amplified by other stresses and disturbances?

In urban areas soils are affected by disturbance in many ways e.g. dumping, altered drainage and hydrologic changes due to roads, pavements and storm water pipes, excessive trampling, forest floor alteration, earth movement for development etc.. The importance of such lines of questioning for the conservation of urban ecosystems thus becomes apparent.

12.1.2. Community organisation : It is known that forests in urban environments differ in both subtle and patent ways from those in less disturbed environments (Bagnall, 1975 in McDonell and Pickett, 1990). For instance urban and suburban forests have a conspicuous proportion of exotic and naturalised species and frequently a lower proportion of certain indigenous species. However little is known about the functional importance of such differences in composition (McDonell and Pickett, 1990). Differences are also apparent in the structure of rural and urban forests (Rudnicky and McDonell, 1989 in McDonell and Pickett, 1990). In urban environments canopy heights are more uneven and the number and connectedness of treefall gaps differs from that in less disturbed forests (McDonell and Pickett, 1990). Similarly, the fauna and its interactions differ in urbanised areas. These conditions suggest that organisation and dynamics of the forest should differ along the gradient (McDonell and Pickett, 1990). McDonell and Pickett (1990) state that once the composition, size structure, and stand architecture are adequately documented, attention can turn to the following questions :

1. Is the regeneration of current or prior dominants limited in forests at the urban end of the gradient?

2. What are the architectural or compositional correlates of regeneration success or failure?
3. What are the biotic, abiotic and anthropogenic causes of regeneration patterns?
4. Do changes in the animal community have direct or indirect effects on plant community dynamics by changing herbivory, predation, or the dispersal relations of the plants?
5. How do human perceptions, values and behaviour affect the dynamics and persistence of forest communities along the gradient?

Given the rapidity with which urbanisation and its associated stresses can proceed, such questioning has obvious value if attempts at urban conservation are to have any chance of success. Thus the inclusion of some examples in this thesis.

12.1.3. Landscape Ecology : McDonnell and Pickett (1990) state that landscape ecology is an empirically young discipline and that the questions that may be asked of it in the context of rural-urban gradients are exploratory, but that such questions may have a stimulatory effect on landscape ecology as a whole. Assuming that landscape elements are more distinct toward the urban end of the gradient, and that the pattern of distinctness can be determined by direct measurement of aerial photographs and maps, illustrative questions may follow upon the pattern analysis produced.

1. Is dispersal of plants, over equivalent distances, more limited in urban than rural ranges of the gradient?
2. Is any such change a direct result of the activities of people or some indirect effect of the size, shape and arrangement of landscape elements?
3. How does size, shape, distance apart and arrangement of patches relate to their species composition and to ecosystem processes within them?

The inclusion of these questions is not arbitrary. While the questions are considered to be useful ones, it is hoped that the difficulties in obtaining answers to such questions may already have been suggested in section 8. While this underscores the need for new approaches in the urban arena at a practical level, it is hoped that the relationship between practice, and the more theoretical and philosophical issues touched upon in sections 9. - 11.1., is becoming apparent. This theme will be developed in sections 13., 14. and 15.1., and leads to further recourse to philosophy in section 15.2., setting the stage for part three of the thesis.

McDonnell and Pickett (1990) propose a conceptual model for the ecology of urban-rural gradients, pointing out that because the

study of ecology along urban-rural gradients is new, a framework to help guide the design and integration of studies is required. These authors maintain that the framework must account for :

1. The factors that constitute urbanisation.
2. The effects of urbanisation on the biota and the physical environment.
3. The resultant effects on ecosystems.

It is hoped that this thesis will contribute to this framework by presenting some ideas on how management may respond to these needs.

McDonnell and Pickett (1990) conclude that given the growth of metropolitan areas, knowledge of ecosystems under urbanisation can only become increasingly important, and that the magnitude and nature of change in the physical, chemical and biotic environments associated with urbanisation provide an unprecedented suite of experimental manipulations for ecologists to utilise. Finally, these authors submit that the study of rural-urban gradients provides a new context in which to integrate humans as critical components of ecological systems, and that such studies will not only contribute to our understanding of basic ecological principles, but are critical to the ecologically sound management of human dominated ecosystems. This thesis aims to make a contribution to this area of study.

13. Theoretical considerations : Ecological Biogeography

The relevance of ecological or reticular biogeography for the conservation of plant communities in urban areas has been discussed extensively by Roberts, D.C. (1990) and Poynton and Roberts (1988) and will not be restated here.

In Durban, existing conserved vegetation types are in most instances both disturbance impacted, and appear to be below the minimum critical areas required for their continued existence as ecologically viable units (Roberts, D.C., 1990). Management requires an understanding of ecological and biogeographical dynamics affecting species and habitat diversity, and in particular, those processes leading to species extinction. Island Biogeography Theory has frequently been used in the question of size/minimum critical area of reserves as it relates area to species diversity. Island Biogeographic Theory alone however, is inadequate in covering the dynamic situation actually found in most areas which come under consideration for conservation (Poynton, 1990). Typically, these are areas seemingly below the minimum critical areas required for the unmanaged survival of the community types concerned. The relevance of disturbance (both as an anthropogenic and natural ecological factor) in understanding community dynamics has implications for the use of Island Biogeographic Theory, as disturbance is correlated with area, and research is needed to enable firmer interpretations and predictions of community

responses to disturbance, particularly in relation to the availability of area (Poynton, 1990). Roberts, D.C. (1990) has clarified both the nature of such research needs, and the usefulness of Island Biogeographic Theory in meeting them (see section 18.1.).

14. Theoretical Considerations : The ecology of disturbance, and patch dynamics.

In urban areas, existing conserved vegetation types appear to be below the minimum critical areas required for their existence as ecologically viable units (Roberts, D.C., 1990). In such urban reserves extinction becomes the dominant process, and in the view of Pickett and Thompson (1978) internal disturbance dynamics thus become the critical design feature of reserves. These authors propose that, particularly with respect to small nature reserves (such as those found in urban areas), reserve design should be based on minimum dynamic area. This they define as the smallest area with a natural disturbance regime which maintains internal recolonisation sources, and hence minimises extinctions. The minimum dynamic area of various taxa will undoubtedly differ, and the minimum dynamic area of a reserve should be defined by the most extinction-prone taxon (Pickett and Thompson, 1978). According to these authors, nature reserves should:

1. be considerably larger than the largest disturbance patch size, including rare patches,
2. include internal recolonisation sources,
3. include different ages of disturbance-generated patches,
4. encompass areas sufficient to support large consumer populations in habitats not made unsuitable by disturbance, and
5. contain separate minimum dynamic areas of each habitat type.

Disturbance in vegetation is generally viewed as an event causing abrupt changes in the structure of a community, displacing it from equilibrial conditions (Pickett and White, 1985). It is presently widely accepted, however, that in many cases stable equilibrial models of communities are inappropriate (Chesson and Chase in Cowling, Le Maitre, Mc Kenzie, Prys-Jones and van Wilgen eds., 1987). The equilibrium-centered view is essentially a static one and provides little insight into the behaviour of systems that are not near the equilibrium. Natural 'undisturbed' systems are likely to be continually in a transient state, and according to Holling (1973), they will be so equally under the influence of man. Particularly in urban environments, disturbance and succession are likely to be ubiquitous landscape features and as a result the landscape becomes a mosaic of successional patches of various sizes. Thus, in urban areas, where disturbance is continuous, pervasive, and occurs in many forms, it is even more likely that conserved 'natural' systems will more often than not be in states of flux.

Internal dynamics in vegetation are generated by patterns of disturbance and subsequent patterns of succession, and may be called patch dynamics (Pickett and White, 1985). In this context, disturbance is best viewed as an event, extrinsic or intrinsic, which results in the removal, addition and/or relocation of biomass or individuals that directly or indirectly creates opportunities for the establishment of new individuals (Sousa, 1984 in Cowling *et al.*, 1987). For this reason, disturbance regimes and the structure and dynamics of communities are inextricably linked. According to Bazzaz (1983) and Denslow (1985) in Cowling *et al.* (1987) the disturbance regime is often a major selective force determining the population structure of communities, and hence the approach to, and type of 'equilibrium' status achieved. In urban areas, and here I refer to Durban, where remaining forests are small, fragmented and isolated from larger areas of continuous relatively undisturbed forest, this is thought to be especially true.

The use of patch dynamics in the design and management of nature reserves thus requires knowledge of the disturbance regime and associated patterns of succession. Because the type of disturbance influences patch characteristics, the effects of different disturbance types is critical information for management initiatives. Additionally, species are differentially sensitive to different types and degrees of disturbance, so that this factor interacts with biology in determining successional pathways and their ultimate results. Prior knowledge of what these results may be is therefore also important for management initiatives. Because the critical factors of patches are their size, and frequency of occurrence in time, the ability to use different types of disturbance as a potential management tool requires active and parallel research, providing managers with continued updated information regarding the effects of different types of disturbance on vegetation, as well as the ultimate successional outcomes of particular natural and man-made disturbance regimes.

In a motivation to the Natal Parks Board, Poynton (1990) considered the following.

1. What constitutes minimum critical area for local plant communities under consideration for conservation.
2. What constitutes acceptable (and perhaps beneficial) levels of disturbance in natural areas in relation to their size.
3. How community dynamics in specific areas develop from man-made disturbance regimes.
4. How disturbance may be used as a management tool.

Research addressing such questions is important for a number of reasons, among them the following:

1. Predictive knowledge is necessary for the success of long-term management strategies.

2. If one considers the landscape to be a shifting mosaic of habitats, then a small reserve that temporarily loses a habitat essential for a certain species may lose that species indefinitely. Thus the minimum critical area for a community type may be the area below which patterns of regeneration on which species depend no longer occur. This consideration highlights the importance of studying edge-to-area effects and the degree to which they reduce the effective size of habitats.

3. If nature reserves are found to be too small, the relieving effects of linking them through corridors need to be established. This raises the question of how wide corridors need to be in order to be functional, as well as how the edge-to-area effect impinges on the efficacy of these corridors.

In the urban setting, vegetation has usually been affected in one or all of the following ways:

1. Species composition of the vegetation has been affected, either by physical disturbance or through the invasion of exotics.

2. Population densities are affected.

3. Population dispersions have been affected through the effects of settlement and development.

Once the effects and outcomes of common disturbance phenomena are known, manipulation of these three factors may make it possible to simulate required disturbance regimes in areas which are too small to include different ages of disturbance-generated patches on which many species depend (Pickett and Thompson, 1978). This simulation may be achieved through the following techniques:

1. Seeding areas in order to alter species compositions and population densities.

2. Burning, cutting and/or mowing in order to either arrest, or promote successional trends, depending on what the trends are, and whether or not they are compatible with management objectives.

3. Physically altering vegetation structure in order to create different successional stages e.g. cutting down large forest trees in order to create gaps in which rarer species may be encouraged to regenerate.

4. Preventing invasion of exotics and removing exotics in order to prevent them outcompeting more 'valuable' indigenous species.

In conclusion; while patch-dynamics and Island Biogeography Theory provide a number of intuitively appealing directives, and while they lend a useful perspective to the urban conservation arena, it should be noted that their final value will rest on the success of research in the specific areas in which management is

to occur. Rather than simply embracing the theory, the challenge is to use it to guide appropriate research. Bearing in mind the contentions of sections 15.1. & 15.2. which follow, the reader is urged to consider that this in itself may pose methodological challenges, thus issuing in the notion of epistemology, another concern of this thesis which is touched upon in section 15.2. and further developed in its final conclusion in section 23..

15. Conceptual considerations bearing on management

15.1. Current understanding of ecosystem processes

"First, ecology is *par excellence* a field in which multiple cause and multiple effect apply."
(Mentis, 1988)

"The basic idea of western science is that you don't have to take into account the falling of a leaf on a planet in another galaxy when you're trying to account for the motion of a billiard ball on a pool table on earth."
(Gleick, 1988)

The complexity of the dynamics of natural multispecies communities is one of the major problems of contemporary population ecology (Godfray and Blythe, 1990). For communities with many species, any description of the population dynamics between and within populations is usually very difficult because of the proliferation of relevant parameters and because their dynamical behaviour becomes qualitatively very complicated (May, 1976). The difficulties of attempting to circumscribe the functioning and determinants of natural systems in terms of time, space and causality are being increasingly suggested by various authors such as Holling (1973), Margalef (1974), Orians (1974), May (1976), Gauch (1982), Hubbell and Foster (1986), Gigon (1987), Pomeroy, Hargrove and Alberts (1987), Mentis (1980, 1988a), Pickett, Kolasa, Armesto and Collins (1988), Gleick (1988, 1990), Godfray and Blythe (1990), Kelly and Harwell (1990), Sheldrake (1990), Macy (1991). Causality, usually defined as the interrelation of cause and effect, is about how things happen, how change occurs and how events relate (Macy, 1991). In science, a major shift is occurring from notions of linear, unidirectional causality to perceptions of dynamic interdependence and nonlinear interconnectedness (Capra, 1982) where phenomena affect each other in a reciprocal or mutual fashion (Macy, 1991).

Biological communities are normally composed of large numbers of interacting species of plants, animals and microorganisms (Godfray and Blythe, 1990). A consequence of the fact that biological systems are subject to time-lags and have spatial

extent, is that the dynamics of biological communities are exceedingly complicated (Godfray and Blythe, 1990). Furthermore, it is reasonable to expect that these complications will be exacerbated in communities exposed to human-induced disturbance. Gauch (1982) concludes that "Necessarily, the finitude of human efforts requires that our studies be both partial and piecemeal." "Communities have countless complex interactions and causal connections, some of which defy observation and analysis" (Elsasser, 1969 in Gauch, 1982).

In his discussion on the usefulness of multivariate techniques in ecology, such as the ones that are used in this study, Mentis (1988a) states:

"Multivariate correlative techniques enabling ampliative inference are suited to prompt yielding of predictive knowledge as opposed to giving insight into function and process. This is valuable for several reasons. With the universality of reductionist causal determinism in disarray, we recognise phenomena for which cause is not specifiable. It is of course possible that we call such phenomena acausal because we have as yet not found the cause. Yet in the spirit of the ascending view that there are no basic biological units with fundamental properties, things cannot be understood in themselves but only in the context in which they occur (Capra, 1975). Furthermore, especially in ecology and socioeconomics we are approaching intractable irregularity. Outcomes emerge from numerous concurrent events, some of which are stochastic and most of which are poorly measurable. No single event need be overriding, yet concurrent events can be strongly synergistic (McNaughton, 1973). The uncertainty arising from this contingency is aggravated by the large number of variables involved, the wide range of their values and hence the greater or lesser uniqueness of every outcome. The tracing of Cartesian causal determinism, even if it exists, is not necessarily within our immediate means."

15.2. Conclusion: the need for philosophical reflection

The above quotation is particularly relevant here in alerting the reader to the need once again for philosophical reflection. Mentis alludes here to the possibility of there being things we cannot know. It is generally conceded in science that perception implies "contact with something other than oneself", or with a "self-existing, real, 'out there' world" which science can set about investigating (Poynton, 1991). Sloan (1979) states that science depends on certain assumptions or presuppositions, "including a belief in order and harmony", or some "underlying logic or order in nature" (Poynton, 1991). Poynton (1991) states that while these presuppositions may seem obvious, all of them can and frequently have been challenged. This gives rise to questions such as "what is truth"; "why can we expect any procedure to explain phenomena"; "can we justify our assumption that there is a continuing out-there world" and "Can we really claim to ever know anything?" (Poynton, 1991).

What is of great importance here is that the debates about whether or not there is a knowable substructure or ongoing order

in nature are closely tied to the epistemological question of how we might go about knowing it. The question of whether the natural world exists independantly of us as something which is in principle knowable, or wether we can only know it in terms of our subjective perceptions arising from it, is a long-considered one in the philosophy of science.

This debate is considered important to this thesis as difficulties and inadequacies in method and general approach at both a theoretical (sections 10. - 15.) and consequently at a practical level (sections 7. - 8.) seem to suggest the need for an epistemological re-orientation in this field. This re-orientation aligns this work closely with a method of philosophical investigation called Phenomenology which holds that the "grasping of 'essences' and 'things in themselves'" (Poynton, 1991) is in fact possible, and that through "spontaneous, direct insight or encounter" (Poynton, 1991), the out-there world can in fact truly be known.

In short, Phenomenology involves the directing of a particular type of attention towards an object (e.g. nature) which is aware of and sets aside all preconceptions about it (Holroyd, 1989), or as Whiteman (1967) states: "an experience attained by a peculiarly enhanced power of reflection, beginning with 'non-attachment', 'recollection' and 'stoppage' (of the current of time), and proceeding to 'essential insight', and a transcendent comprehension, by which details of intelligible structure in any experience can be held changelessly in view....."

While Phenomenology's status as a method of investigation underlies its epistemological importance, it is notable that Phenomenology has a distinctly mystical component, and therefore an added ontological dimension. To quote Whiteman (1967): "In its higher reaches it is characterised by an unmistakable kind of unity, (my emphasis) and becomes, in the words of Liebniz, 'the knowledge of necessary and eternal truths'". Notions of unity and interrelatedness, however couched they may be in philosophical terms, recall to mind the enduring insights of ecology and should be considered relevant by those concerned with ecological research. The apprehension of relatedness and unity also has a strong bearing on the inclination to care. In the opinion of this thesis there is no reason why, as ecophilosophers, we should not seriously consider Phenomenology's ontological dimension while at the same time, as scientists, making use of its epistemological approach. In fact, in the conservation arena, an integration of both Phenomenology's ontological and epistemological insights can be strongly argued for, and shall be in this thesis.

PART 3.

In keeping with the theme of sections 9., 15.2. and the conclusion to section 14., this thesis now hopes to show that theoretical and methodological problems are also encountered in pursuits which may generally fall outside the ambit of philosophising, such as modelling and management. Sections 16.

and 16.1. are included to indicate some of the uncertain theoretical ground on which modellers and managers must tread, (as does section 15.) and how this affects the suitability of models, particularly in the urban environment. This thesis makes no pretensions to expertise in modelling, and sections 17. to 17.8. attempt to show, in as unopinionated a way as possible, what may be good and bad about models as tools in both a practical and philosophical sense. The justification for the section on modelling is primarily felt to lie in section 17.8. where once more, philosophy is seen to be instructive in an area of scientific endeavour in which philosophical assumptions are arguably manifest, but seldom acknowledged. It is noteworthy too, that the final paragraph of section 14. could equally apply as a conclusion to the modelling section, in that the confirmation and testing of theories, and model predictions may pose epistemological problems.

While not directly philosophical in vein, a thesis of this nature would be incomplete without reference to management and monitoring. These sections are also included however, to show that these subjects can be linked to the broader themes of this thesis. These are: that theoretical consideration is necessary (section 18.1.), that the requirement for caution with method is evident (section 18.2.), that ecology needs to be thought of in a more expansive sense (section 18.3.) and that uncertainty needs to be tolerated (section 18.4.). In confirmation of the above notions, the complexity and difficulty of monitoring is discussed in section 18.6.. These perspectives are also offered in an attempt to confirm the need for critical appraisal of current approaches, as well as the need for openmindedness in the consideration of suggested alternatives.

16. Population dynamics and species interactions

"Chaos should be taught, he argued. It was time to recognise that the standard education of a scientist gave the wrong impression. No matter how elaborate linear mathematics could get....May argued that it inevitably misled scientists about their overwhelmingly nonlinear world"

--- Gleick, 1988 quoting Robert May ---

Processes operating at the level of individual organisms can determine the properties of populations, communities and ecosystems (Koehl, 1989). Also, the coupling of multiple environmental factors affect the performance of individual plants. Koehl (1989) maintains that only once such coupling is better understood will a unified quantitative theory develop that can be related to models of plant geographic distribution or community composition. There appears to be a growing recognition that processes that occur at the level of individuals can form the basis for constructing a theoretical framework with which to interpret the properties of populations or communities. In any given habitat large numbers of species influence each other through direct pairwise interactions and through indirect

interactions mediated by intermediate species, processes or substances (Levin, 1976 in Levin, 1989). Because it is impractical to observe all the potential interactions among all species and processes, ecological research generally involves the simplifying assumption that much of the complexity of nature is either unimportant or can be subsumed within a few summary variables (Tilman, 1989). The study of population dynamics and population interactions is thus, of necessity, a process of ecological abstraction. Ecologists attempt to find, through empirical observation (*), experimentation and theory, the critical subset of parameters and interspecific interactions that are needed to describe and predict ecological patterns (Tilman, 1989). Increasing attention is being given to the question of how the process of ecological abstraction might best proceed.

(*) Note: Tilman's use of the word 'empirical' connotes its philosophical meaning i.e. "regarding sense-data as valid information", or "deriving knowledge from experience alone." (The Concise Oxford Dictionary, 1990). Tilman's use of the word is both imprecise and misinformed. If its philosophical content is implied, then it is inaccurate to create the impression that ecologists have traditionally used empirical observation free of prior theory; a critical glance at the history of science reveals, if anything, the opposite. Furthermore, the use of empirical observation is inconsistent with the process of abstraction with which Tilman associates it. This is not trivial as shown in sections 15.2. & 19.2.1..

Tilman (1989) emphasizes the problems inherent in interpreting interactions in multispecies communities with a discussion of what he refers to as indirect effects. He cites, as an example, the following. Of all the food-web linkages that exist, probably the most overlooked is that of decomposers (see e.g. Pomeroy, Hargrove and Alberts, 1987). One of the indirect results of the life of a decomposer is the supply of mineral nutrients that are both required by and often constrain plants. Variations in the supply of these nutrients can impact on competitive interactions among plants (Tilman, 1989) and thus all processes influencing decomposer species are potentially important (Tilman, 1989). If, for instance, the litter of different plant species differed in its suitability as food for decomposers, this could lead to changes in nutrient mineralization rates (Pastor, Naiman and Dewey, 1987 in Tilman, 1989). Tilman maintains that in theory, this could form a positive feedback loop that would magnify initial differences in local species composition, leading to multiple stable equilibria.

In similar vein, increasing evidence is accumulating that physiological and life historical behaviour can provide an understanding of population growth, size and age structure, coexistence, competitive outcome and successional turnover (e.g. Foin and Jane, 1977; Bazzaz, 1984a; Mooney and Chiariello, 1984; Bazzaz *et al.*, 1986 in Bazzaz and Sipe, 1987). The potential explanatory power of physiological ecology at the ecosystem level will vary with the dynamics of the system in question (Bazzaz and Sipe, 1987). Higher-level behaviour cannot be understood through

reductionist assembly of lower components and neither can it be fully understood without the mechanistic detail of physiology (Bazzaz and Sipe, 1987). These authors are of the opinion however, that physiological and life historical strategies of species may serve as a starting point for population and community behaviour in moist, close-canopied forests.

The specifics and accuracy of such conjecture aside, the examples are instructive in their suggestion of how subtle, and difficult to detect, relevant factors may be.

The literature on plant population dynamic theory and plant population dynamics and species interactions is copious, highly theoretical, and suffused with uninvestigated problem areas which render the validity and applicability of much of our understanding tenuous. Bazzaz and Sipe (1987) maintain that ecologists seem, during the last decade, to have reached a plateau in the attempt to construct a body of theory that is realistic and general enough to serve as a paradigm for their science. These authors maintain that the effectiveness of major generalisations concerning such topics as succession, competitive niche divergence, diversity-stability and r-K selection has been questioned by theoretical disproof or frequent case exemption. They continue to point out, however, that few concepts of similar stature have been developed since about 1975, despite the fact that there have been some heavily researched issues e.g. disturbance and plant-herbivore interactions. During this period, much has been learnt about the workings of populations, communities and ecosystems, but even more has been learnt about the limitations of traditional ways of viewing and studying ecological interactions (Saarién, 1980; Levin, 1981; Salt, 1983 in Bazzaz and Sipe, 1987).

Ecologists are gradually becoming more comfortable with the heterogeneity, stochasticity and ungeneralizability of many ecological phenomena (Johnson, 1977; Simberloff, 1980; Strong, 1983 in Bazzaz and Sipe, 1987) and new ways of thinking about the complexity of ecological systems, largely borrowed from the physical sciences, are becoming increasingly popular (Bazzaz and Sipe, 1987) as shown in section 21..

16.1. Equilibrium population sizes: fact or fiction?

The regulation of plant populations, particularly of long lived plants such as trees, is very poorly understood (Hubbell, Condit & Foster, 1990). By regulation, these authors refer to the idea that there are clear limits to population size, and that the processes generating these limits operate in a density-dependent manner (Silvertown, 1982 in Hubbell *et al.*, 1990). In principle, density-dependent processes can affect rates of birth, death and migration (all of which are critical in the small, isolated and disturbed ecosystems of urban areas) or any combination of these rates (Hubbell *et al.*, 1990). In practice density-dependence is a problematic concept to apply to plants (Hubbell *et al.*, 1990) while the enormous plasticity of plant growth means that the fecundities of individuals at the same site may vary by several

orders of magnitude (Harper, 1964 in Pacala, 1989). This makes it difficult to specify what a mean population size should be (Harper, 1964 in Pacala, 1989).

The concept of an equilibrium population size upon which tests of density-dependent regulation of populations rest, has been attacked by Wolda (1989) who provides an argument which may well have great relevance in the highly and variously disturbed landscapes with which this thesis is concerned. Wolda (1989) maintains that such an equilibrium is a purely theoretical construct whose existence in the field is debatable and whose value cannot be measured. In summary, Wolda's argument centres around the fact that an equilibrium is supposed to fluctuate in time, but the extent of the fluctuations relative to those of population size is unknowable. Wolda (1989) maintains that it is impossible to separate a fluctuating population size from a fluctuating equilibrium value and from fluctuating deviations from an equilibrium value. Because it cannot be determined whether a given population size is above, at, or below equilibrium, the course of population size is unpredictable and density-dependence tests cannot be expected to produce useful results.

Argument about whether or not equilibria in population sizes exist aside, it is questionable what, if anything, can be done with the equilibrium concept (Wolda, 1989). Those supporting the theory of density dependent regulation assume populations fluctuate in size around an equilibrium value, the equilibrium population size being the value at which the number of individuals does not change and to which it will return after a disturbance (Wolda, 1989). It has long been realised however, that the equilibrium itself is not, spatially or temporally, a constant. It is not inconceivable that disturbance- exacerbated phenomena, themselves having a multiplicity of spatial and temporal components, would keep this supposed equilibrium value in a state of constant flux, rendering it practically meaningless. Wolda himself states that different populations of the same species may have different mean densities because their environments are different, and, as environmental factors vary in time in one particular population, so does the equilibrium. This view seems to be supported by Hubbell *et al.* (1990) who point out that although competition is often an especially localized phenomenon in plants, which compete mainly with their immediate neighbours for limited light, water and soil nutrients, the spatial scales over which competition actually operates are poorly known.

In a paper addressing the question of the prevalence and importance of density-dependence in limiting the abundance of tree populations in a species-rich neotropical forest in Panama, Hubbell *et al.* (1990) could find no evidence for density-dependent regulation. These authors generated data from population dispersion, growth and survival patterns, and recruitment patterns to conclude that, with the exception of one or two extremely abundant canopy, and possibly midstorey species, the "vast majority" of species were nowhere near the densities at

which density-dependent feedback would limit further population growth. These authors did however concede: "our conclusions must all be regarded as tentative because although we have monitored the forest for a decade, this is only a small fraction of the lifespan of many of its member tree species."

Wolda (1989) concludes that an equilibrium cannot be measured, irrespective of whether or not it exists, and that the concept is devoid of any practical ecological content; something better left to the theorists until it can be reconciled with practical considerations.

In attempting to conserve impacted tree populations in small areas where insight is that much more difficult to gain (see section 20.3.), the meaningfulness of the equilibrium concept in practical terms calls into question the usefulness of the concept of disturbance as a force altering this so-called equilibrium. When so plagued by contingency, such theorisation needs to be treated with caution when used in the management arena. This should be borne in mind when this thesis advocates the possibility of other approaches.

17. Modelling

"Typically, in ecology, there are few data
and poor understanding relevant to the
problem to be modelled"
(Mentis, 1988)

"Since forest islands are to a great degree
a consequence of man's land-use, they are a new
type of natural system for which we have a limited
data base enabling us to infer long-term system
behaviour. Models represent a valuable adjunct
to studies on the fundamental nature of such ecosystems"
(Shugart and West, 1980)

17.1. Introduction

While modelling approaches would be difficult in the Durban area for technical, organisational and financial reasons, and while modelling can be criticised, it is probable that modelling software will become cheaper and more accessible and that its usefulness in management situations will become further clarified as our understanding of the forests increases. For these reasons it is going to be discussed in this thesis. Although modelling approaches are inconsistent with some of the other ideas in this thesis, the out-of-hand dismissal of any tools or approaches is seen as being naive, as is any form of option-foreclosure in diversity of approach.

Modelling is becoming increasingly important as a means of structuring research such that it can assist in identifying key

questions (Saunders, Arnold, Burbidge and Hopkins, 1987). Models can also aid communication and provide a means to make the most of available knowledge and experience, and may also have application in the planning process and day to day management (Saunders *et al.*, 1987). Ambitious as the above assertions may seem, the difficulties presented in sections 17.2. and 17.3. also mitigate against ignoring its possible role.

17.2. Modelling as a response to statistical difficulties

Field ecology poses logistical problems with respect to replication and temporal and spatial scales (Mentis, 1988a). While statistical texts prescribe that samples must be independent to justify resort to inferential statistics, avoiding the pitfalls in achieving independence (i.e. by committing various forms of pseudoreplication) is not easy (Mentis, 1988a). In part, this is because we live in a world full of unique places (Hinds, 1984 in Mentis, 1988a). Whether or not one can achieve true replication (in space or time) in dynamic, highly disturbed, internally heterogeneous environments, seems to be a question that ecologists have not yet asked. If true replication cannot be practised, then inferential statistics (as opposed to multivariate correlative techniques) are not valid (Mentis, 1988a). "Consequently numerous situations arise in ecology where there is a bundle of inseparable correlates and the attempt to unravel cause and effect is hindered by inherently poor falsifiability" (Mentis, 1988a).

17.3. Modelling as a response to time constraints

With respect to time scales; the slow, subtle and complex processes operative in ecosystems, and the infrequency of critical events, are believed to require long-term studies for elucidation and testing (Mentis, 1988a). There are however numerous obstacles to long-term studies, including the sustained commitment to money, time, manpower and facilities necessary for their completion (Mentis, 1988a). Furthermore, many pressing environmental problems need prompt answers in a society which operates largely on a short-term planning horizon (Mentis, 1988a). For these, and other reasons (see Mentis, 1988a), Mentis suggests that in terms of cost:benefit ratio and research flexibility, rapid iterations of conceptualisation and testing, in a modelling context, may be superior to long-term studies (Mentis, 1988a).

Mentis (1988a) concludes that "The criteria of falsifiability accordingly rest here not so much on predictive quality but rather on compliance with background theory (it is not made clear how one decides which background theory is relevant), the degree to which implications of a short-term nature are corroborated and the internal consistency and parsimony of models." Mentis (1988a) also notes that the mere act of constructing a model is of well-known heuristic value.

Throughout this section, only models thought to have potential application, or those raising ideas/concepts thought to be

relevant to the situation at hand i.e. small highly disturbed forests in the greater Durban area, are considered. The elaborate mathematical, abstract, and highly theoretical nature of many models renders them inappropriate for consideration in the Durban context, as do the difficulties in their application, and especially, necessary interfacing with required empirical studies.

17.4. Models of individual plants distributed in space

Spatial interactions strongly influence plant community structure and dynamics (Busing, 1991). Plant population dynamic models including spatial locations of individuals and spatially local interactions have yielded some interesting theoretical insights, and ideas.

The discrete-cell construction, precise mathematical formulation, local applicability, and underlying structure and parameterisation of such models will not be discussed here. Only the ideas that the models raise will be considered.

1. Dispersal ability is a strong determinant of the outcome of competition because it affects the spatial distribution of juveniles, and because interjuvenile competition is spatially local (Schmida and Ellner, 1984 in Pacala, 1989).
2. Random fluctuations in fecundity can, in some cases, overwhelm competitive asymmetries and maintain the diversity of a plant community (Chesson and Warner, 1981; Schmida and Ellner, 1984 in Pacala, 1989).
3. Where dispersal distances in plants are short, this may facilitate coexistence by increasing the degree of interspecific spatial segregation. This is because with short dispersal, distributions change form through time due to the aggregation of siblings about their mother and the differential effects of intra- and interspecific interference (Pacala, 1986a in Pacala, 1989).
4. The outcome of competition is in part determined by relations among several spatial scales, including neighbourhood radii, mean dispersal distances, and the spatial scales of environmental heterogeneity (Pacala, 1986a, 1987, in Pacala, 1989).

17.5. Models including within-population variation in plant size - the effects of plasticity

Models investigating the population dynamic consequences of within-site variation in plant growth (Aikman and Watkinson, 1980 and Holsinger and Roughgarden, 1985 in Pacala, 1989) are based on assumptions rendering them of little value in disturbed environments. These assumptions are:

1. Models incorporate continuous-time within-season plant growth.
2. Fecundity is proportional to plant size and density-dependent growth and mortality.

3. Within-population variability is included by assuming that growth rates vary among individuals according to a normal distribution.

It is assumed that it would take considerable research effort to ascertain the suitability of these assumptions for Durban forests. It is probable that this requirement alone could render such models inappropriate.

These models suggest the following:

1. Plant size distributions become increasingly skewed during the growing season.
2. Equilibrium population sizes (commented on in section 16.1.) and between-season population growth rates are increasing functions of the variance in plant growth rates.
3. Plasticity can affect the outcome of competition between plant species i.e. the more variable of two species will competitively exclude the less variable, all else being equal.

(The above points are all in Pacala, 1989)

May (in Pacala, 1989) notes that the high degree of variability in fecundity in plant populations represents demographic stochasticity in itself.

17.6. Gap models

Gap models simulate forest dynamics by accounting for the establishment, annual growth in height and diameter, and mortality of every single tree on a small model plot corresponding to the zone of influence of a single dominant tree in the canopy (Horn, Shugart and Urban, 1989). These authors are of the opinion that such models are effective at time scales of decades to centuries (although precisely what this means is not clear), and at spatial scales typically in the range of 0.1 to 10 hectares. It is relevant to point out here that the entire Pigeon Valley forest is only 10 ha in extent, while Burman Bush is 50 ha and Virginia Bush 38 ha. Furthermore, the claim of gap models to stability over large time scales is unconvincing unless disturbance regimes are equally constant over such scales.

Gap models have successfully predicted qualitative patterns of species composition and structure, and have even had some quantitative success. They are particularly useful for simulating the dynamics of forests with mixed ages and/or mixed species of trees, and for exploring patterns of forest dynamics at time scales that are long enough to prohibit direct observation (Horn, Shugart and Urban, 1989). Such properties are not necessarily of immediate value where the premium is on taking decisions in the short term.

Intuitively appealing as gap models are (especially in disturbed forests where gaps are common), gaps themselves are complex.

Gaps, by definition, overlap with closed canopy situations, and complex microenvironmental gradients develop between the two. The multilayered structure of the forest alters the ranges and spatio-temporal variations in air and soil temperatures, windspeed, ambient [CO₂], irradiance, soil moisture, nutrients and relative humidity (Bazzaz and Sipe, 1987). The nature of gap and understory microenvironmental gradients are functions of disturbance frequency, size and magnitude (Bazzaz and Sipe, 1987). Gap size, shape, orientation, and the remnant community interact to produce enormous heterogeneity among forest gaps in patterns of physical and chemical fluxes (Ricklefs, 1977; Bazzaz and Pickett, 1980; Denslow, 1980; Bazzaz, 1983, 1984b; Pickett, 1983; Brokaw, 1985 in Bazzaz and Sipe, 1987).

Given the above, how easy it would be to establish the suitability of gap models to forest situations in the greater Durban area is a moot point.

17.7. Simulation models

An alternative to the modelling approaches discussed above is to include autotrophy, spatial dynamics, and plastic growth in complex computer simulations. Such models are typically based on submodels of the growth, mortality and reproduction of individual trees as affected by light, water and nutrients, in which a population model is constructed from many modelled trees (Pacala, 1989). Trees are stratified by height and are located in one or more spatial cells. Further submodels govern the dynamics of resources in each cell, taking into account the effects of shading on the light available to each tree. Models may also take into account factors such as fire, storms and seed predation (Pacala, 1989).

Forest simulators have been developed primarily to predict dynamics in specific forest systems, and their complexity and system specificity render them of little use in theoretical explorations of the factors controlling distribution and abundance in general (Pacala, 1989). Simulations are designed such that they sacrifice simplicity and explanatory power for increased accuracy of system-specific predictions (Pacala, 1989). A further problem is that, as in the case of many forest modelling applications, neither detailed environmental data at a micro-spatial scale nor quantitative historical stand data are available (Harrison and Shugart, 1990).

Several general insights do, however, emerge from forest simulation models (Pacala, 1989), these are:

1. It is possible to estimate many parameters in models of even diverse forest communities.
2. Models, in some cases, have remarkable predictive power.
3. Species diversity does not collapse catastrophically in models lacking spatial heterogeneity in physical processes.

These insights have emerged from models based on relatively simple, undisturbed Northern Hemisphere forests with low species diversity, and in which small selections of trees were modelled. Their relevance for small, species rich and highly disturbed forests is questionable.

Ecosystem-level simulation models pose problems for predicting long-term effects. The major difficulty is that model builders should have both species-specific and system-wide stress-response data to hand during model development (Dyne, 1981; Kendall, 1982 in Ted Hinds, 1984), so that the model reflects known behaviour under stress, rather than mere extrapolations (National Research Council, 1981 in Ted Hinds, 1984). The accumulation of this sort of knowledge in Durban forests would be extremely difficult, if it is possible at all. Even if it were theoretically possible, personpower and financial constraints would prove prohibitive. Furthermore, in the current state of knowledge it is not known how much research will be required, and therefore what the cost:benefit ratio will be, in developing a predictive model (Mentis, 1988a). However, direct testing of our perceptions of long term phenomena is not necessarily the best course (Mentis, 1988a) (refer to section 17.3.).

17.8. Conclusions

Plant population dynamic models accounting for sedentary habit, spatially local interactions and plastic growth demonstrate that each of these three characteristics have significant population dynamic consequences (Pacala, 1989). These models have led to new hypotheses about the structure and dynamics of plant communities and Pacala maintains that because plants are sedentary, it is both possible and practical to determine experimentally the merits of different models and to test hypotheses that emerge from the theory.

Pacala (1989) states that the further development of spatially explicit models is essential because interactions among plants are inherently spatial. In the vertical dimension, competitive asymmetries associated with shading may affect secondary succession as well as within-site variation in plant size. In the horizontal dimension spatial heterogeneity in resource availability is caused by plants as well as by spatial variation in physical processes. Pacala maintains that this "biotic" spatial heterogeneity may maintain successional diversity in nature. While Pacala's comments are of interest, spatially explicit modelling poses its own difficulties. A major disadvantage is the difficulty of calculating a meaningful biological measure of competition, and in the excessive computer time and storage space required to execute such models (Munro, 1973). One of the greatest obstacles to the operational use of such models is the requirement for tree spatial information; such information is expensive to acquire and is generally unavailable for any but the most intensively monitored permanent sample plots (Munro, 1973).

Pacala concludes that plant population dynamics are affected by factors other than competition for abiotic resources. Amongst

these he lists seed predation, herbivory, disease, pollination and mycorrhizal associations. In Pacala's view, autotrophy, sedentary habit and plastic growth promise to bring as much to the theory of these interactions as they have to the theory of plant competition.

Mentis (1988a) points out that in a field critically short of both data and understanding, the mere formulation of models and accessing of existing data can enable fresh ways of approaching problems (Mentis, 1988a). It is interesting to note, however, that decisions in ecological management are often made in practice on the basis of qualitative data and an individual's accumulated experience (Starfield and Bleloch, 1983). In such instances, the links between the data and the final decision are usually implicit, and, according to Starfield and Bleloch (1983) ecological models have not generally been successful in elucidating this implicit process. The representation of field indicators often requires an unreasonable and unattainable level of detail in the model (Starfield and Bleloch, 1983) and this creates a two-way gap between modellers and managers - the first in that managers cannot convert their experience into data for the model; the second in interpreting model output in terms of action (Starfield and Bleloch, 1983). Starfield and Bleloch state that "Efforts to quantify have perhaps deflected attention from the need to live with and exploit qualitative data...." Such commentary is broadly accordant with that of Mentis (1988a), with respect to the value of observational data, Hill and Gauch (1980) in connection with their comments on ecological insight, and Whiteman (1986) on the nature of experiencing (see section 19.2.1.). It is also seemingly consistent with Peat's (1991) views on the irreducibility of natural phenomena, and Steele's (1989), on the conceptual opaqueness of computer solutions (see section 21.).

Starfield and Bleloch (1983) have attempted to show that expert systems provide a computer framework for organising qualitative data and investigating the rationale behind decision-making in ecological management. It is possible that this would be a more profitable course to follow than attempts at modelling. Whether the case for the use of expert systems in ecological management is strong or weak can only be discovered through practice (Starfield and Bleloch, 1983).

18. Management

"The matter of generating and testing solutions to problems is the province of scientific management. The use of the term 'scientific', from the Latin, 'to know', is unfortunate because nothing in the physical or biological sciences can be known with certainty."

(Mentis, 1980)

18.1. Overview

The aims of urban open space conservation and the strategic demands for accomplishing such aims have been dealt with in depth by Roberts, D.C. (1990), and do not require restatement. It is relevant to point out, however, Robert's adoption of a biogeographically oriented approach, the aim of which is "the design and establishment of a network of open spaces capable of supporting an ecologically representative, diverse, dynamic and self perpetuating example of the local indigenous flora and fauna within the city...." This chapter will concentrate mainly on the specifics of managing forest plant communities.

An understanding of the relevance of the Theory of Island Biogeography to the conservation of small fragmented biotas is critical in urban conservation. While it is not the aim of this thesis to review the theory, it would be a disservice to the topic not to mention the areas of enquiry this theory has brought to our attention, and into which it has generated insight.

The theory has been reviewed by Simberloff (1988), Diamond (1982) and Roberts, D.C. (1990) who includes in her treatment of its importance, the following general considerations :
(for citation and details, see Roberts, D.C., 1990).

1. The species-area relationship (MacArthur and Wilson, 1967).

2. A review of the geometric design principles proposed by Diamond (1975), which are concerned with three themes:

a) The benefits of single large reserves as opposed to groups of smaller ones of the same total area., under which Roberts, D.C. (1990) considers the following.

Target species for conservation
Edge-to-area effect
Minimum critical area
Genetic inbreeding
Trophic cascades/community structure
Habitat diversity
Patch dynamics
Rescue effect
Competition and disease

b) The best spatial arrangement of a system of reserves.

The need for corridors
Corridor characteristics
Corridor dimensions
A hedge against the taxon cycle

c) The optimal shape of reserves.

In its broadest sense, management is a synthetic/interdisciplinary concern, requiring, in the city, a

consideration of the links between its economic, social, and ecological substructure, and its spatial organisation (Yanitsky, 1984). The need for a strengthening of the links between a complex of social and natural sciences, and the development of methods for ecologically orientated planning of urban areas has been confirmed in Durban by Roberts, D.C. (1990).

18.2. Biology and management

The very idea of management contains inherent, tacit, and more often than not dangerous suppositions about how much we know (Page, 1990). The application of ecosystem theory, and ideas such as succession, diversity, stability and stress, to conservation and management practice, are poorly established (Regier and Cowell, 1972; Holling, 1973; Mentis, 1980; Page, 1990), although the effects of this can to some extent be offset as suggested in section 18.4.. Such sceptical appraisal is not given here for its own sake, but rather as a frame of reference to alternative approaches proposed later.

18.3. Management strategy

Prerequisites for management include legislation, a policy framework, and physical 'on the ground' management itself (Muir, 1990). Strategic organisational demands include the establishment of an adaptive management approach, the setting of clearly defined objectives, the inclusion and cooperation of relevant parties, and the balancing of objectives with available management resources (Muir, 1990).

While such commentary is both non-biological and trite, successfully bringing management into the realm of workability depends on common purpose, open channels of communication, and formalisation of the organisational structures through which management decisions are taken and implemented. At present, much of the philosophy and initiative in management and planning in the Durban area rests on personality and a fortuitous mixture of people; no grassroots structures exist in planning circles whereby continuity of approach, or even priority is ensured. Management initiatives are often retarded by divisive use of organisational structures and the operation of personal politics. Bureaucratic structures and overly hierarchical organisational frameworks result in separate agents defeating each other's purposes. Changing climates of staff motivation may also affect the operation of management bodies, as well as their failure to recognise the need for expertise and to liaise effectively with organisations external to their own. Roberts, D.C. (1990) and Muir (1990) found these considerations to be central to the problem of conservation in the Durban and KwaZulu regions respectively, and it is increasingly being realised that conservation efforts in Africa fail not only through lack of biological knowledge but rather communicative, organisational and cultural knowledge (Nott, pers.comm.). Such opinion reaffirms the idea in section 12.1. that an expansion of traditional ecological concerns is necessary. If these issues remain trivial to biologists, then conservation initiatives themselves are trivialised.

18.4. Adaptive management and monitoring

Conservation biology is both an applied science and a crisis discipline (Soule and Wilcox, 1980; Soule, 1985) and management initiatives within its ambit can seldom await the results of studies that may not yield solutions (Mentis, 1980). Tolerating uncertainty is often necessary (Soule, 1985) and "progress is essentially adaptive, where one learns to manage and manages to learn simultaneously" (Mentis, 1980). This interdependence of knowledge and its application is fostered through frequent iteration among goals, problems, observations, hypotheses and tests (Mentis, 1980), a process known as adaptive management (Holling, 1978; Mentis, 1980).

18.4.1. Why adaptive management?

Adaptive management is consistent with the views of section 18.2. for the following reasons :

1. Ecology is a conceptually young science dealing with unique complexity, and because of this few tested ecological principles have emerged (Ray, 1982; Pomeroy, Hargrove and Alberts, 1987; Page, 1990). Adaptive management enables managers to reduce the impact of ignorance by detecting flaws in our understanding of ecological processes (Page, 1990).
2. It is frequently difficult to isolate the causes of, or driving forces behind, particular ecological events, and many phenomena are covariable, and have correlates which are not causal factors (Page, 1990). Unless the correct variables are being monitored, the causal factors remain elusive. Adaptive management helps to identify variables which should be monitored (Page, 1990).
3. Misconceptions about ecosystem behaviour bias management strategy. Adaptive management allows managers to continually reassess not only the validity of assumptions regarding how systems behave, but also the land use goals for the area (Page, 1990).
4. Principles governing the behaviour of systems are frequently counter-intuitive (Page, 1990). Adaptive management facilitates acceptance of counter-intuitive logic, leading to the discovery of new principles (Page, 1990).
5. Community responses to disturbance often have lags, e.g. with disruption, the species composition of forest islands inevitably lags behind changing forest island patterns (Burgess and Sharpe, 1981). This results in effects being observed long after causes have disappeared (Page, 1990). The rates of many ecological processes are slow and human memory is incapable of accurate recollection of the state of complex ecosystems when attempting comparisons separated in time (Page, 1990).

Without the thorough knowledge of the system that can only be gained by long-term monitoring and regular processing of results,

sound management decisions cannot be made, and effects (especially secondary effects) of management actions cannot be determined (Ray, 1982; Page, 1990). Given the difficulties and challenges highlighted by this thesis thusfar, it is logical that such an approach should in principle be argued for in the Durban area.

18.5. The how of adaptive management

18.5.1. Introduction

Research is not something discrete from, or incidental to management. Research and monitoring are an integral part of management (Miller, 1982; Tinley, 1987).

Research can never occur too early in management, and ideally should form part of the selection process for reserves (Miller, 1982). Miller (1982) argues that certain key ecosystem processes are compromised by the containment of incomplete ecosystems within the boundaries of reserves and that research needs to focus on what these key processes might be. Furthermore, research should investigate new management actions, focusing on practical approaches that are available to managers for manipulating ecosystems, including the cost and effectiveness of alternative management techniques. Research should identify processes for monitoring (Miller, 1982). Monitoring can never cover all the components and processes of conserved ecosystems. For this reason research should define those minimum geographical areas, ecological processes, and indicator species needing to be monitored to ensure adequate description of conserved areas (Miller, 1982). Miller (1982) states that "Monitoring should not become a research responsibility. Rather monitoring should identify new questions requiring research, which, in turn, should provide new insights into and possibly improved approaches to monitoring."

18.6. Monitoring

"Mankind's failure to use ecological principles to minimize negative impacts of human activities is arguably the most important failure of the twentieth century"

(Karr, 1987)

"Good design is needed, not fancier statistics"

(Green, 1984)

The complexity of ecosystems poses a variety of choices for ecological monitoring measurements (Hinds, 1984). No single selection is correct for all purposes and among the approaches that may be considered, each level of organisational complexity, from individuals to total systems, has strengths and weaknesses for detection of ecological effects (Hinds, 1984; Ridsdill-Smith,

1987). In monitoring contexts, current thought about the ecosystems level approach is ambiguous (Hinds, 1984). The systems-level approach is conceptually correct, but depending on the measurement strategy, may be prohibitively expensive (Hinds, 1984). The possibility of replication at the system level in field conditions is almost totally unexplored (Hinds, 1984) and fraught with difficulty (Mentis, 1988a). Karr (1987) advocates the use of ecological guilds as a way of using ecological principles in a more integrative fashion in monitoring. Karr (1987) maintains that to be most effective, monitoring should encompass individual (health), population (structure and/or dynamics), community (structure) and ecosystem (function) attributes, claiming that the use of indicator species and diversity indices is simplistic, and conceptually invalid respectively. Hinds (1984) states that different sub-system levels of organization may be useful, depending on the objective of monitoring. These are:

1. Single species.
2. Guilds or functional groups i.e. groups of taxonomically unrelated species that make their living in a similar fashion.
3. Trophically linked species e.g. predator-prey-decomposer linkages.

Hinds (1984) lists a number of specific possible approaches, but concludes that ecological science cannot currently predict their long-term usefulness without more experience (Barrett and Rosenberg, 1981 in Hinds, 1984). As a result, variety in approach and design is to be expected, and encouraged (Hinds, 1984).

Roberts, D.C. (1990) maintains that "the trick is to define and analyse groups of species in ways that are simultaneously practical, realistic and revealing." She concludes that a judicious mix of autecological studies, and broader, more inclusive community-level approaches appears to offer the best basis for rational conservation action.

Ecological monitoring designs have at least three major difficulties (Hinds, 1984), these are:

1. Selecting and quantifying specific biotic conditions or activities within the continuous spatial and temporal flux that characterises life.
2. The statistical difficulty of specifying appropriate replication standards in a world full of unique places (see section 17.2.).
3. Expense.

Furthermore, ecosystem response and recovery needs to be characterised in relation to the particular qualities of the disturbance the ecosystem is subject to, including intensity, frequency and duration of the disturbance, and, how the action of the disturbance is partitioned throughout the ecosystem in time and space (Kelly and Harwell, 1990).

18.7. Monitoring guidelines

These guidelines are provided for the following reasons.

In areas where disturbance is pervasive, and always occurring anew, some formally established system of monitoring is necessary. At the very least, consistent monitoring ensures that the forests are looked at on a regular basis, and this thesis will argue, that it can be through the process of looking, that knowledge is gained. This idea is explored more fully in the conclusion to the thesis in section 23..

Miller (1982) proposes the following considerations with respect to monitoring :

1. The objectives of a monitoring programme should be clearly defined. Decisions regarding the selection of species, areas and processes for monitoring, and subsequent use of data generated, are dependent on the setting of clear objectives (Miller, 1982).
2. Monitoring programmes should focus on key processes or species. Most monitoring programmes focus on the demographic status of populations, or on the state of the soil or vegetation i.e. they do not focus on ecological processes *per se*.. Miller (1982) maintains that ecosystem functioning is more sensitive to changes in rates of ecological processes than it is to changes in their products. For this reason, monitoring focussing on rates of ecological processes, such as birth and death, or immigration and extinction, will better provide indications of impending changes in ecosystem behaviour (Miller, 1982). Miller's (1982) ideas in this regard are possibly a little simplistic (see section 18.6.)
3. The genetics of rare species need to be monitored. It is necessary to identify and monitor populations which may be susceptible to inbreeding depression. Usually these will be species with small effective populations (Miller, 1982).
4. The requirements for accuracy, precision, repeatability and comparability need to be clearly established. A sound statistical approach is necessary if managers are to be able to distinguish real changes from variations due to sampling errors, and if results are to be at all reliable (Miller, 1982). Hinds (1984) maintains that difficulties in detecting long-term ecological changes stem from the amount and kind of information that may be required to produce valid sampling designs. Hinds (1984) states that an adequate long-term method cannot evolve from mere repetition of an arbitrarily chosen field method and that problems with interpretation, replication, variability and cost may frustrate such straightforward approaches. N.B. the statistical, sampling, field-sampling variability and replication considerations discussed by Hinds (1984) would profitably merit further consideration, despite being too detailed for a project of this scope.

5. Monitoring should be carried out with sufficient frequency to be able to detect change in time for management action to be taken. Generally, when monitoring key species, sampling frequency will be determined by the frequency of perturbations, the average generation time of the species, and its capacity for rapid population change (Miller, 1982). It is quite possible that in forests, for instance, certain non-woody species should be sampled more regularly than woody species.

6. Analysis and interpretation of data should follow closely after their collection. Information gleaned from monitoring needs to be made available as quickly as possible; too often data are stored, and the opportunity to detect, interpret, and respond to changes is lost (Miller, 1982).

7. Monitoring is an integral part of management. Research should be responsible for identifying monitoring needs, and information gained from monitoring should help to clarify research objectives. In this way, both pursuits remain relevant (Miller, 1982).

Most long-term studies of populations are now undertaken in remnants of what were once more extensive habitat, and the need to consider the unique characteristics of ecological systems on habitat islands thus becomes relevant (Ehrlich and Murphy, 1987). These can include high edge-to-area ratios, lack of microhabitat heterogeneity, and other characteristics which can bias study results. In such environments, Ehrlich and Murphy (1989) argue, some species, although not threatened, may be keystones in remnant ecosystems or indicators of ecosystem condition.

Noble and Slatyer (1980) propose the use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. These life history attributes (vital attributes) are used to categorise species as specific types depending on:

1. Method of arrival and persistence of a species at a site during and after disturbance.
2. Ability to establish and grow to maturity following disturbance.
3. Time taken for them to reach critical stages in their life history.

Noble and Slatyer (1980) maintain that the interaction between various species, based on their species types and life stage attributes, yields a replacement sequence which depicts major shifts in composition and dominance which will occur following a disturbance. The degree to which vital attributes were robust properties of species would need to be explored in relation to different disturbance frequencies and intensities, and to the seasonal time of disturbance (Noble and Slatyer, 1980). Noble and Slatyer's scheme is based on certain assumptions, some of which may preclude its applicability in the Durban situation. Further investigation would be required to establish its usefulness.

19. Sampling, data, and their interpretation

19.1. Introduction

Without accurate conceptualisation, problems cannot be solved. Central to the solving of problems, or generating of perspectives in ecology, is the choice of data collected, the manner in which they are collected, and how they are analysed. This is not trivial, as methods of analysis reflect in part one's assumptions about how natural systems work, the extent to which they are amenable to investigation, apprehension and understanding, how one might best proceed in generating understanding, how sure one can be of one's facts and results, and how one might go about refining and applying them.

At the outset, studies should be thought through from objectives and selection of approaches, through methods, design and data analysis to interpretation and inference (Mentis, 1988a). Although innumerable texts prescribe how to design an experiment and how to collect and analyse data, only rarely is guidance offered on the selection of the type of broad approach to be used, on the nature of inferences to be drawn and on the limitations and implications of these (Mentis, 1988a).

19.2. Ordination

Problems in community ecology often require the inferring of species-environment relationships from community composition data and associated habitat measurements (Ter Braak, 1986).

Multivariate analysis is a branch of mathematics that deals with the examination of numerous variables simultaneously (Gauch, 1982), providing statistical methods for the study of the joint relationship of variables that contain intercorrelations (James and McCulloch, 1990), thereby providing a methodology for elucidating the complex interactions observed in community studies (Goldstein and Griegal, 1986; Digby and Kempton, 1987).

Ordination, in the case of this study, Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980), is an ampliative technique (Mentis, 1988a) which has been used in numerous instances in ecology to generate insight through specifying the occurrences of species in community samples and enabling workers to speculate on factors governing plant community distributions e.g. Bredenkamp, Theron and Van Vuuren (1983), Lloyd (1989), Deall and Theron (1990), Shackleton, Mentis, Mcenzie and Granger and (1991), in Natal forests, Moll and Woods (1971), Moll (1980), in the examination of disturbance-mediated successional relationships (Halpern, 1988), the discernment of trends in vegetation change over time (Foran, Bastin and Shaw, 1986), for investigating specific questions about the response of species to environmental variables (Ter Braak, 1986, 1987) and investigating condition and trend in urban forest islands (Hobbs, 1988).

19.2.1. Multivariate techniques; Ordination and scientific method

"This idea, that theory dictates
what one sees, cannot be stated too strongly"
-- Eldredge and Gould, 1972 --

"Don't think, but look!"
-- Wittgenstein --

Multivariate methods are essentially descriptive (Mentis, 1988a, James and McCulloch, 1990) ampliative and inductive in nature (Mentis, 1988a), and rely on the use of strong inference (see section 19.3.). Most often, multivariate methods are used in an exploratory sense, when questions are still imprecise (James and McCulloch, 1990), as they so often are in ecology (Mentis, 1988a). This exploratory stage can be a very creative part of scientific work, and can suggest causes, which can then be formulated into research hypotheses and causal models (James and McCulloch, 1990). James and McCulloch (1990) maintain that: "In the general scientific procedure, descriptive work, including descriptive applications of multivariate analysis, should not be relegated to a status secondary to that of experiments. Instead it should be refined so that research can proceed as a combination of description, modelling, and experimentation at various scales." The state of current knowledge in ecology may be insufficient for postulating non-trivial hypotheses, and conceptual problems concerning the formulation of appropriate falsifiable hypotheses, as well as establishing the grounds on which a given hypothesis is to be refuted, abound (Mentis, 1988a). For this reason, the inductive element in ordination is significant. As suggested above, hypothetico-deductive approaches in ecology are beset by certain conceptual, logistic, and even ethical problems (see Mentis, 1988a). Inductive (as opposed to hypothetico-deductive) approaches may be used to generate hypotheses, or as an end in themselves in the form of description. Mentis describes such techniques as 'ampliative', implying that the content of inferences drawn is not present either explicitly or implicitly in the premises (Mentis, 1988a). This approach is considered initially consistent with the presuppositionlessly observant, or phenomenological approaches to investigation gaining increasing stature in both scientific research and philosophy (e.g. Wolf, 1984; Poynton, 1985; Whiteman, 1986; Holroyd, 1989). As an approach, it has exciting, albeit unexplored possibilities, and is apposite in disturbed, stochastic forest environments where traditional methods seem to be more at risk (Pickett and White, 1985) (refer also to sections 7. & 21.). Whiteman (1986) is a contemporary philosopher of science who cautions against introducing "overbeliefs into the description of an experience or in the interpretation of the description". Whiteman (1986) states: "One may be so anxious to make sense of the experience that one slips into using terms which imply the experiencing of things not actually experienced

or which set the whole in a metaphysical or scientific framework which was not part of the experience itself. In short, the description of an experience and our analysis of it, must be strictly phenomenological. And this demand laid on evidence must be satisfied before we tackle the problem of evaluating the probable 'reality' of the experience which it purports to describe."

The appreciation of a practising ecologist of the idea of a face to face analysis arising from direct encounter is alluded to by Mentis (1988a) who states that ampliative techniques "which identify patterns in our data and enable the formulation of hypotheses or models based on the data, are not severely constrained by some preconceived view of how the world is" and that the prospect of developing the inductive method "will aid in the important practical question in ecology of how to extract information about system functioning from purely observational data."

Mentis (1988a) cautions against seeing ampliative inference as a cure-all. Like hypothesis-testing, it is also subject to conceptual, logistic and ethical problems which constrain acquiring data sets with sufficient statistical degrees of freedom for inference to be drawn i.e. it amplifies the what rather than the how. Ampliative techniques are also theory-laden to the extent of the parameters chosen, the methods of estimation and analysis used, and the more or less testable assumptions made (Mentis, 1988a). Mentis (1988a) suggests that, given certain considerations (see Mentis, 1988a) inductive and hypothetico-deductive approaches need not be mutually exclusive, but may be used in tandem. Mentis (1988a) states that when a correlative pattern is established, its predictive capability is often improved by probing the processes underlying the correlates and isolating the apparently important ones for more rigorous testing, and investigation using experiments (Mentis, 1988a).

Lastly, Mentis (1988a) admits that, in drawing attention to the inductive approach in ecology, "I might be guilty of imprecision in describing how it is adopted", but argues that to a degree "such vagueness must remain because of the unavoidable partly inspirational nature of discovery." The "very creative" nature of scientific work, when questions are still imprecise, and multivariate methods are being used in an exploratory sense, early in an investigation (James and McCulloch, 1990), is also notable here, as is the subjective content to modelling (James and McCulloch, 1990). In possibly similar vein, Goldstein and Grigal (1986) state that results of many numerical classifications and ordinations can be interpreted statistically if certain statistical properties of the multivariate universe under study can be established. These authors maintain however, that for ecological systems this is usually impossible, and that where statistical inferences are not possible, results should be interpreted in a qualitative manner, to gain insights into the system, to generate meaningful hypotheses, and to design experiments. In their paper on detrended correspondence analysis, Hill and Gauch (1980) seem to allude to a similar

outlook; concluding that - "DCA consistently gives the most interpretable ordination results, but as always the interpretation of results remains a matter of ecological insight.....". Verification of the above views is intimated by contemporary philosophers and biophilosophers like Wittgenstein, Husserl, Whiteman and Sattler (in Poynton, 1991) who stress the difficulties of observation unclouded by theory-laden presuppositions, but propose that when insight, intuition or conceptual analysis is effective, that it is "superior to all theories" (Whiteman, 1967).

It is important to note that even philosophers such as Whiteman do not reject hypothesizing out of hand, conceding that working hypotheses are a legitimate and valuable "heuristic and practical tool" (Whiteman, 1967).

This section is included in this thesis in an attempt to show, within the constraints of an M.Sc. project, that philosophy has relevance for methodological debate in ecology. In a young discipline in which method has been traditionally reductionist and positivist in character, and in which impoverished theoretical debate still abounds, the significance of new philosophical paradigms is arguably important, if not always immediately obvious (see section 21.). This section also sets the scene for one of the conclusions of this research.....that there is a philosophical justification for naturalists (as opposed to scientists), arguably those best equipped for observational analysis, to contribute to creditable science.

19.3. Bad features of D.C.A., and the dynamical systems perspective of vegetation theory

There is disagreement in the literature as to the value of using DCA above other ordination techniques (see Lloyd, 1989). Hill and Gauch (1980) cite examples of field data on which it has been tested, and its application in vegetation ecology has become widely established. Certainly there are no readily available, clearly superior techniques. For relatively objective community-centered ordinations, Detrended Correspondence Analysis has been found to be most effective and robust, "especially with very heterogeneous and difficult data sets" (Gauch, 1982).

Multivariate techniques can be criticised in that judgments about results can be dangerously close to circular reasoning (Goldstein and Grigal, 1986; James and McCulloch, 1990). It is tempting, but invalid, to leap directly from the exploratory stage, or even from statistical tests based on descriptive models, to conclusions about causes, when no form of experimental design figured in the analysis (Gauch, 1982; James and McCulloch, 1990). Similarly, although analysis of ecosystem structure using only species-data can give penetrating insights, there is also some degree of circular reasoning involved in this approach (Goldstein and Grigal, 1986). For this reason, species and environmental analyses are complementary, and are best used jointly in explaining spatial and temporal patterns in vegetation, although even this approach is plagued with potential difficulty

(Goldstein and Grigal, 1986). (See Goldstein and Grigal (1986) in section 19.7.).

By implication, D.W. Roberts (1987) contests this kind of thinking, proposing instead, a dynamical systems perspective on vegetation theory. Central to the dynamical systems perspective is that neither vegetation nor environment can be treated as an independent variable (Roberts, D.W., 1987). The current state of both the environment and the vegetation composition depend on the previous states of both components, and, accordingly, vegetation analysis should not employ the concepts of dependent and independent variables.

D.W. Roberts (1987) argues that current underlying models of many vegetation analyses are based on the algebra of multivariate functions. One of the underlying assumptions of such models is that, given a multivariate expression of the environment, there is one vegetation composition which is best adapted to the site (Roberts, D.W., 1987). The task of vegetation analysis is then viewed as fitting the vegetation to environmental gradients and simply attributing the failure to do so to noise i.e. an "environmental determinist" approach (Roberts, D.W., 1987).

Mentis (1988a) points out that merely collecting data and performing ampliative techniques leaves uncertain the degree to which patterns and hypotheses thus generated are descriptors of a particular data set, or the extent to which they have predictive value. In highly disturbed, patchy environments, this is thought to be especially true, as is the contention of D.W. Roberts (1987).

Quoting Greenacre (1984), Mentis (1988a) discusses three methods of judging the predictive quality of hypotheses generated with multivariate correlative techniques. These are:

1. By removing a random fraction of the data, repeating the analysis and seeing how stable the pattern is.
2. Including additional data, repeating the analysis and seeing how the pattern alters.
3. Repeating the analysis on a fresh and independently collected data set.

Mentis (1988a) points out that while extensive corroborative testing of predictions confers confidence in a model, the model is never entirely secure.

It is suspected that these suggestions would be of limited value in the forests with which this study was concerned. High degrees of internal heterogeneity, coupled with varied and ubiquitous disturbance events and effects, all of which confound environment-vegetation interrelations, may well result in suggestions 1 - 3 producing substantially different results from which little additional insight could be gained, beyond that of amended description. For what it is, however, description is not to be undervalued. (see recommendation 3., section 22.).

19.4. Outliers and uncommon species

The most persistent difficulty with DECORANA is that of coping with outliers and discontinuities in the data set, the only way of coping with extreme outliers being to remove them (Kershaw, 1973; Hill and Gauch, 1980).

Species ordinations obtained by DCA are generally less satisfactory than stand ordinations (Hill and Gauch, 1980). Kershaw (1973) considers reduction in the total variation in the data to be particularly effective if rare species are removed from the analysis. Kershaw (1973) suggests that if most of the information relating to the structure of the ordination is carried by the most abundant species, that the "rare species can simply be ignored" (Kershaw, 1973). This particular claim on the part of Kershaw is treated here with some skepticism on account of the fact that rare species are often important indicators of community type, especially in changing, disturbed environments where species presence/absence may be a dynamic, transient phenomenon. Furthermore, one cannot be sure which species are considered rare, whether they are rare for natural, or disturbance-induced reasons, or of the extent to which they are downweighted by the programme.

19.5. Noise

The biological causes of noise are complex and include chance distribution and establishment of individuals, animal activity, local disturbances and environmental heterogeneity at scales below that of the sample area (Gauch, 1982). Conceivably, all of these phenomena may be altered and/or exacerbated by disturbance.

19.6. Interpretation of axes, and further criticisms of ordination

A problem that can never be eliminated with DCA is how to interpret the axes (van der Maarel, 1979 in Hill and Gauch, 1980). Multivariate techniques allow plant community composition to be related to abiotic environmental factors but most often both the community composition and abiotic environmental factors are multidimensional and internally correlated, requiring that both data sets be subjected to multivariate methods (Goldstein and Grigal, 1986). Given the intractable complexity of the physical environment, this in itself poses substantial difficulties (see section 20.2.2.1.).

Although multivariate procedures for constraining ordination axes such that they are linear combinations of environmental variables are now available e.g. Canonical Correspondence Analysis (Ter Braak, 1987), the collection and analysis of accurate physical data in unhomogeneous environments suffering a high degree of physical impaction is problematic.

Gauch (1982) comments on the difficulties that may be encountered in attempting to correlate species and community distributions, making the following points:

1. Important environmental and historical factors need to be identified and practical methods for measurement devised. Important factors are often far from obvious and factors that are important in only a few releves can be especially problematic.

2. In nature, no factor ever varies alone (McIntosh, 1970 in Gauch, 1982). Environmental factors tend to form complexes. This raises the question of which factor in a complex of factors principally affects the distribution of individuals or communities. This picture is further complicated by the fact that environmental factors may correlate not only with other factors but with specific complexes of other factors, all of which will vary in their means, variances, maxima and minima over time.

3. Environmental (and disturbance) factors vary on many scales, both spatially and temporally, and this makes any sampling scheme effective for some factors but not for others (Gauch, 1982). Environmental and historical factors are usually assessed using the same size scale as is used for gathering the community data. If, for instance, one were attempting to study biogeographical dynamics affecting species and habitat diversity, this would be inappropriate as these two scales are incommensurable.

4. Because community data, as well as the environmental and historical data they are compared to, are usually both multivariate, when the results are interpreted, the difficult task of comparing two sets of data, both multivariate, is encountered (Gauch, 1982).

Canonical Correspondence Analysis is an efficient ordination technique when species have bell-shaped response curves or surfaces with respect to environmental gradients (Ter Braak, 1986). However, in the forests on which this study focused, considerable research effort would have been required to separate species responses to environmental variables from those to disturbance factors. In small, fragmented, disturbed and isolated forests it is doubtful whether the presence of bell-shaped response curves could be demonstrated to exist, even if such a species response were theoretically possible. Furthermore, it is argued that species responses to environmental gradients may well be unimodal, and individualistic, and that in such cases traditional ordination techniques do not give reasonable results (James and McCulloch, 1990). Individualistic plant responses, confusing to interpret in themselves, are likely to be rendered even more unclear where vegetation is simultaneously reacting to disturbance events. While community species composition is an integral function of a stand's environment, it is also an integral function over time (Goldstein and Grigal, 1986). Gauch (1982) states that when objective eigenanalysis ordinations are used, environmental interpretation consists of relating community gradients (as summarized from community data by ordination), and environmental gradients, but that environmental factors include disturbance and historical factors. Hence species composition can reflect past and present

environmental conditions (Goldstein and Grigal, 1986) as well as species responses to the shifting mosaics of disturbance which characterise landscapes (Urban, O'Neill and Shugart, 1987).

D.W. Robert's (1987) incisive observation that the relationship between vegetation and environment is relational rather than functional, is relevant here, as are the many empirical studies suggesting that community stability depends on properties of the component species rather than on emergent properties of systems themselves (Halpern, 1988; Petraitis, Latham and Niesenbaum, 1989). While the environment may determine which plant species can occur, it does not determine which plant species will occur (Roberts, D.W., 1987). Roberts, D.W. (1987) thus suggests that the interpretation of vegetation as the direct product of a complex of physical and site factors is erroneous, and points to the importance of quantifying the role of plants in modifying the environment, and the subsequent response of vegetation to the modified environment. Mentis' (1988a) contention that there are no basic biological units with fundamental properties, and that things cannot be understood in themselves, but only in the context in which they occur, is noteworthy here.

Halpern (1982) used DCA to examine successional relationships among six understorey communities exposed to a gradient of disturbance intensity. Ordination was used through time i.e. euclidean distances between pre- and post-disturbance samples in ordination space were used to compare community resistance to disturbance, and long term recovery. Ordinations revealed increasing compositional change with disturbance intensity and initial rapid floristic changes away from predisturbance composition. Halpern (1982) concluded that variation in the long-term response of communities reflects complex interactions between species life history, disturbance intensity, and chance. In South African forests, Van Daalen and Geldenhuys (1988) maintain that lack of long-term data series precludes discrimination between human and natural causes of forest change, stating that conclusions about driving forces for change in forests can only be tentative. Successional processes following human disturbances seem to be the main driving force and overshadow other possible trends (Van Daalen and Geldenhuys, 1988). Given the views of Halpern (1988) and Van Daalen and Geldenhuys (1988), it is conceivable that when investigating such communities, it is simplistic to invoke environmental variables alone in explaining species associations.

Pielou (1984) comments that DECORANA (the fortran programme which performs DCA) removes two sources of error that arise when nonlinear data are ordinated by ordinary reciprocal averaging i.e. the arch and scale contraction effects. Its defect, however, is that it gains these advantages by deliberately flattening the arch and applying local adjustments to the scales of the axes (Pielou, 1984), sometimes introducing further distortion (James and McCullogh, 1990). Pielou (1984) remarks that if these effects are truly mathematical artefacts, devoid of ecological meaning, then it is desirable to remove them, but that overzealous correction of suspected defects may lead to the

"unwitting destruction of ecologically meaningful information." Wartenburg *et al.* (in James and McCulloch, 1990) endorse Pielou's concern, arguing that the arch effect is not an anomaly, but an inherent property of data that represent transitions in species abundances as one passes through localities more favourable to some species and later more favourable to others.

Bredenkamp, Theron and Van Vuuren (1983) and Lubke, Morris, Theron and Van Rooyen (1983) found transitions in plant communities to occur along gradients of soil nutrients, texture and pH, and moisture and nutrients respectively, while Shackleton, Granger, McKenzie and Mentis (1991) found coastal grassland communities and subcommunities to be correlated with soil conductivity, altitude, and organic matter and marginally correlated with amounts of sand and clay. Lloyd (1989) used discriminant function analysis to select the linear combination of soil variables that best characterised the differences between seven communities on the Vaalputs radioactive waste disposal site in Bushmanland. The best discriminating habitat variables were, in order of importance, exchangeable Na, exchangeable K, soil pH, exchangeable Ca, exchangeable Mg and soil depth. Lloyd (1989) points to the fact that discriminant analysis provided an indication of the combination of variables best characterising the differences between communities, as well as the relative importance of each variable, while DCA illustrated the relationship of plant communities to one another, thus providing an indication of the gradients in these variables.

In contrast to such seeming success, Everard (1986), who was able through the application of TWINSpan to twenty quadrats of *Podocarpus latifolius* forest to identify eight separate vegetation subcommunities, was unable to explain the grouping of quadrats produced despite measurements of the following environmental variables.

1. Exact location within the forest patch.
2. Altitude.
3. Aspect.
4. Gradient.
5. Topographical features within the forest.
6. % soil moisture.
7. pH
8. % organic content.

19.7. Conclusion

It is not the intention of this thesis to decide finally on the merits of ordination, but rather to show that opinions about its use are equivocal. Its usefulness may vary, and depend in large measure on site-specific conditions. Forest studies have shown both interrelationships between vegetation and site characteristics (Geldenhuys and van Laar, 1980), and significant correlations (van Laar and Geldenhuys, 1975).

It is significant that Fuzzy-set theory has been applied in ecology and ordination. This suggests a recognition of the fact that many concepts in ecology are imprecise, and points to the attraction of theoretical approaches in ecology that are able to cope with objects which are imprecisely defined (Equihua, 1990). Ecologists, it would seem, have caught up with Nietzsche at last!

In concert, the thinking of Mentis (1988a) and Roberts, D.W. (1987) (section 19.3.) constitutes a substantial critique of the uses of ordination in disturbed environments. Similarly, Gauch (1982), Goldstein and Grigal (1986), Roberts, D.W. (1987), Mentis (1988a), Halpern (1988), Petraitis *et al.* (1989) and James and McCulloch (1990) (section 19.7.) together appear to suggest to me its further inadequacies for use in such environments.

20. A Broad-scale conceptual analysis of the problem to which techniques, data and stats are pertinent.

20.1. Introduction

For structure in forests to be characteristic, or for trends to become apparent, a degree of homogeneity is assumed. In the absence of such homogeneity, and/or where forests are small and highly disturbed, problems with sampling, interpretation, and the use of statistical/mathematical descriptive and quantitative techniques occur. This makes management difficult, necessitating exploratory and adaptive management approaches, and the need for detailed and ongoing descriptive approaches to gaining knowledge about forests.

While research is required at many levels for adequate understanding of forest management, Roberts, D.C. (1990) states that "the most comprehensive understanding of the general function of natural systems is likely to arise from research posed by management following the assessment of monitoring results."

The importance of theory, experimentation and modelling has been alluded to. Further consideration of these would be appropriate to an ongoing study, and will not be dealt with specifically in this conceptual analysis.

20.2. Forest ecology

20.2.1. Introduction

The literature on forest ecology is too large to provide an overview of the hypotheses contained in it, other than in a few specific, relevant instances. In view of the importance of theory (as discussed in section 10.) it is a disservice to neglect it, but it is also difficult to ascertain the relevance of much existing theory to the forests under study.

The spatial structure and dynamics of species-rich tropical forests suggests that chance and biological uncertainty play a major role in shaping the population biology and community ecology of tropical tree communities (Hubbell and Foster, 1986; Brokaw, 1987; Halpern, 1988). Ecological biogeographers, too, are increasingly turning to historical perspectives to interpret community structure, or are at least becoming aware of historical explanations for distributions which were previously attributed to ecological processes (Bond, 1989). While direct comparisons between tropical and Coast Lowland forests (Cooper, 1985) may be invalid, the biotic environments shaping the life histories of trees are inherently statistical in nature e.g. gap formation is fundamentally and inherently a random process.

20.2.2. The ecology of disturbance and patch dynamics

Most recent work on forest dynamics suggests that the ontogenetic niche (seedling regeneration niche), i.e. conditions in the earliest phase of establishment, are of central importance in controlling plant establishment and abundance (Bond, 1989). The fact that most forest trees require 'gaps' of some kind for successful establishment and maturation is widely attested to in the ecological literature e.g. Denslow, 1980; Pickett, 1983; Brokaw, 1985; Pickett and White, 1985; Popma and Bongers, 1988; Hartshorn, 1989; Schupp, Howe, Augspurger and Levey, 1989). Accordingly, the importance of microsites is discussed by Whittaker, 1974; Grubb, 1977; Whittaker, Morris and Goodman, 1984; Ehrlich and Murphy, 1987; Bazzaz and Sipe, 1987 and Williams-Linera, 1990.

To understand the composition of forests, therefore, one must understand the nature of gaps and gap forming processes or patch dynamics, and the kind of interactions that impinge on the juvenile stages of trees (Grubb, 1977; Pickett and White, 1985; Denslow, 1986; Hubbell and Foster, 1986 in Bond, 1989). If conditions governing establishment are significant, then presence of a species may be determined by presence of the right kind of gap providing the right kind of regeneration niche (Bond, 1989).

Natural disturbances have come to be recognised as powerful ecological forces (Platt and Strong, 1989). Gaps in forest canopies increase light levels and change other characteristics of the environment sufficiently to influence the dynamics of

populations of trees (Platt and Strong, 1989), forest architecture and forest composition (Brokaw, 1985). Thus forest dynamics are driven by disruption, with heterogeneity in disturbances hypothesized to produce forests that are internally heterogeneous and ever-changing (Platt and Strong, 1989). Disturbance has demonstrated effects on community characteristics, including richness, dominance and structure, and the functional attributes of communities (Pickett and White, 1985). Nutrient cycling and energetics respond, too, to disturbance (Pickett and White, 1985). Thus, even mature forests have been described as shifting mosaics of different-sized patches cycling through gap, building and mature phases (Watt, 1947; Whitmore, 1975; Oldeman, 1978; Bornman and Likens, 1979 in Brokaw, 1985).

Gaps differ in their size, shape, frequency of formation and the rate at which they fill (Denslow, 1986 in Bond, 1989) and these several axes of variation may generate a variety of different niches (Denslow, 1987 in Bond, 1989). Thus, gaps of different sizes and stages of regrowth are an important source of heterogeneity in the composition and dynamics of tropical forests (Brokaw, 1985), and gap formation produces patches that can differ markedly in tree population dynamics, species composition and growth rate (Brokaw, 1985b). The idea of dynamism is important here. A description, by definition, is static, and therefore of little value unless it is ongoing.

The patch dynamics concept suggests that to interpret forest composition and dynamics one must study regrowth in gaps of different sizes (Brokaw, 1985).

Intuitively pleasing as it is in highly disturbed environments where gaps and patches are compellingly obvious, it should be noted that the patch dynamics perspective, although important, must be considered jointly with the many other factors affecting plant distributions and abundances, both within, and irrespective of gaps. These include competition (e.g. Anderson, 1989), treefalls (e.g. Brokaw, 1982), dispersal (e.g. Augspurger and Franson, 1988; Augspurger, 1984; Denslow, 1987), life history characteristics (e.g. Finegan, 1987; Halpern, 1988), pollination (e.g. Hubbell, Condit and Foster, 1990), balance between immigration and extinction, dispersal corridors (e.g. Geldenhuys, 1989), phenology (e.g. Grubb, 1977), germination requirements (e.g. Grubb, 1977), reproductive rates (e.g. Denslow, 1987), seed dormancy characteristics (e.g. Brokaw, 1985), growth rates (e.g. Denslow, 1987), predation (e.g. Schupp, 1988), pathogens (e.g. Augspurger and Kelly, 1984; Augspurger, 1984), chance (e.g. Hubbell and Foster, 1986; Halpern, 1988) and stochastic replacements (e.g. Horn, 1974), seedling survival, and whether or not species are habitat generalists or specialists (e.g. Hubbell and Foster, 1986). The effects of many such phenomena are difficult to quantify, and do not lend themselves to study in the short term. As Roberts, D.C. (1990) states; the need for long term monitoring in urban areas "involves a further change to the existing pattern of research whereby most researchers are constrained to short-term projects as a result of funding, design, continuity and interpretive problems"

(Strayer *et al.*, 1986; Wallace and Moore, 1987 in Roberts, D.C., 1990).

Furthermore, the perspectives of the authors cited above suggest the vagaries of interpretation one encounters in sampling and interpretation in disturbed forests i.e. what aspects of vegetation dynamics are a reflection of disturbance and what are attributable to other processes, and how does one separate the two (see also section 11.1.). Sampling theory is loosely tied to our understanding of vegetation dynamics, and when plants are simultaneously integrators of their disturbance histories (anthropogenic and other), their physical environment, their biological properties and chance, all at different scales, then attempting to design a sampling approach which usefully elucidates vegetation dynamics, and separates the abovementioned processes, is difficult. This relates particularly to section 7. on sampling.

In the small, internally heterogeneous, historically, variously and highly disturbed forests with which this study was concerned, the contention of Lieberman, Lieberman and Peralta (1989) is, at the outset, relevant. Notwithstanding the substantial complexity of gaps themselves (see section 17.6.) these authors suggest that: implicit in the designs of most studies of gaps is the notion that the non-gap is a standard against which gaps can be evaluated. Lieberman *et al.* maintain that, notwithstanding the conceptual appeal, considering forests as a Swiss cheese of gaps and non-gaps does not even begin to do justice to the daunting complexity of real forests. Lieberman *et al.* maintain that non-gaps are as heterogeneous as gaps. Canopies vary in composition and location above the forest floor, as well as in thickness and foliage density, and are riddled with openings varying in size from a few square centimetres to a hectare or more (Hartshorn, 1980; Sanford *et al.*, 1986; Popma *et al.*, 1988 and Lieberman and Lieberman, 1989 in Lieberman *et al.*, 1989). This remarkable structural heterogeneity is not only the result of the dynamic history of the stand, but is the background against which new disturbances occur (Lieberman *et al.*, 1989). This is why it is necessary to ordinate on structural attributes such as cover.

20.2.2.1. Plant biology, soil, and the vagaries of scale

Spatial heterogeneity and plasticity are largely responsible for the difficulties plant ecologists face in formalising community interactions (Levin, 1976; Schaffer and Leigh, 1976; Pacala and Silander, 1985 in Bazzaz and Sipe, 1987). These and other problems have led Botkin (in Bazzaz and Sipe, 1987) to suggest there are fundamental limits to what is knowable about community interactions as complex as succession. It is arguable that this uncertainty would extend to how community dynamics in specific areas, and associated patterns of secondary succession, develop from man-made disturbance regimes. The seeming importance of microsites does little to add to the knowability of the picture. At the spatial scale of the size of a seed lying in the ground, soil environments alone are very heterogeneous (Whittaker, 1974). Notwithstanding different microsite characteristics themselves e.g. light, moisture, depth to rock; the physical and chemical

properties of soil suggest small-scale variation that may highly significant to seedlings (Whittaker, 1974). Nor can one assume the physical environment to be homogenous in space and time. This raises the problem of estimating the relative contributions towards the maintenance of diversity, of environmental heterogeneity vs. disturbance (and other factors) (Connell, 1979). Connell (1979) maintains that hypotheses regarding this problem would be very difficult to test on account of it being impossible to be sure one had chosen the relevant niche axes to study. The ideas of Roberts, D.W., (1987) are again pertinent here; as well as those of section 19.7.. This heterogeneity in the microenvironment, combined with the extreme subtlety of germination requirements, can itself determine the number and variety of seedlings that are recruited from the seedbank into a population of growing seedlings (Harper, 1977).

Changes in the gross physical environment, e.g. temperature, soil type, compaction and exposure, change the frequency of safe sites in the soil environment, altering the probabilities of a seed forming an established seedling, and the representation of different species (Harper, 1977). (see comments on indirect ordinations and the collection of environmental data). Furthermore, at the microsite scale, populations and communities are composed of individuals that respond uniquely to any given shift in energy or resource flux (Bazzaz and Sipe, 1987). Such uniqueness is due to genetic individuality, developmental status, and/or the differing attributes of each plant's neighbourhood (Bazzaz and Sipe, 1987). Individual responses vary too, with organism stature, longevity, life history and physiology (Bazzaz and Sipe, 1987). Thus a single disturbance may be imperceptible for one organism (or population) and disastrous for a second organism (population) at the same site (Bazzaz and Sipe, 1987). The causal events that determine whether a seed forms a seedling, and the fate of that seedling, are usually untraceable when the plant has developed, and the real causes of distribution and abundance will often be missed when mature vegetation is studied (Harper, 1977). This perspective is important for section 7. on sampling. Simply by their scarcity, rare species are more likely than common ones to disappear from, or not be recorded in forest plots, but, equally, may reappear from new immigration or from a bank of seedlings or saplings in the population below enumeration size (Swaine, Lieberman and Putz, 1987). Besides this, subsequent interactions between organisms that have been differentially affected by disturbance events may be quite different when compared to predisturbance dynamics i.e. the composition and development patterns of the remaining community may have been significantly altered (Bazzaz and Sipe, 1987).

20.3. Some conclusions

The ideas contained thus far in section 20. have implications for some of the conventional ways of studying forests. Plant ecologists traditionally describe tree populations in terms of

their size or age structure, but forests are dynamic entities that change as a dynamic mosaic (Shugart, 1990) and there are dangers in assuming that size and age are closely related (Harper, 1977; Shugart, 1990; Muir, 1990b; Swaine and Hall, 1986 in Swaine, Lieberman and Putz, 1987). Indeed, there is ample evidence that tree size and age are only weakly related in natural forests (Harper, 1977; Veblen, 1986 in Shugart, 1990). In fact, populations may develop towards a characteristic size structure irrespective of their age structure (Harper, 1977). Demographic studies show that most forests have age structures reflecting past disturbances (Harper, 1977), but the size of a forest and the spatial scale of heterogeneity or homogeneity in forests can confound the interpretation of diameter distributions (Shugart, 1990) for many reasons e.g. the scale at which the data are assembled to produce the diameter distribution curves (Shugart, 1990) and the fact that very different phenomena can produce equivalent results in terms of the changes in the numbers of trees in a particular size class (Shugart, 1990; Harper, 1977; Silvertown, 1982 in Muir, 1990; Crawley, 1990; Harper and White, 1974). In drawing attention to the need to account for spatial scale in interpreting diameter distributions, Shugart (1990) suggests that tree-to-tree interactions are likely to be most easily interpreted using diameter distributions drawn from surveys at smaller spatial scales. Shugart (1990) points out, however, that sample variation, particularly for large trees is greater at these same scales, while Crawley (1990) notes that few data sets are sufficiently extensive to allow simultaneous estimation of spatial and temporal variance in population density in such a way that the relative magnitudes of spatial and temporal variance can be compared. Ogden (1985 in Whitmore, 1988) reports that differential mortality (such as one may expect in highly disturbed forests) may lead to size distributions totally obscuring age structure. In the Durban forests, where one is sampling isolated, fragmented remnants of once more extensive populations, and where one is working in very small areas, the problems mentioned by Shugart (1990), Crawley (1990) and Ogden (1985) are significant ones. These problems aside, Muir (1990b) notes that even in the most intensively managed systems, accurate species specific distributions for all species are practically unobtainable due to the level of sampling required. The problem of sampling intensity is all the more acute when one considers clumped or unusual distributions (Muir, 1990b), as well as the breakdown in normal dispersal and reproduction that affects population structure and dynamics when fragmentation of natural landscapes occurs (Roberts, D.C., 1990). Muir (1990) notes that size-class distributions represent snapshots in time and as such may be useful tools in assessing the instantaneous condition of a population but have no reference points for comparison or for relating deviations from expected curves to disturbance factors. Muir (1990) adds that for size-class distributions to be interpreted accurately they need to be backed up with studies of species autecology and reproductive strategies while van Dalen (1990) states that our present knowledge regarding aspects such as spatial distributions, the multi-stemmed nature and the cyclic regeneration patterns of trees exclude their general application in forest management.

This situation is further complicated by the fact that fragmentation of the landscape may have led to alterations in natural disturbance regimes which may alter the long-term functioning of communities (Roberts, D.C., 1990).

One of the major problems faced by researchers, therefore, is to assess the extent to which disturbance regimes experienced by fragmented natural systems differ from those in continuous vegetation (Hobbs, 1987 in Roberts, D.C., 1990) and to determine how relevant the maintenance of natural disturbance cycles is to management goals (Roberts, D.C., 1990). Even if it were possible to determine the nature and periodicity of natural disturbance cycles, logistically the management of disturbance regimes may pose severe difficulties in fragmented landscapes (Roberts, D.C., 1990). It is unlikely that small remaining forests will lend themselves to management for retaining original communities in anything like the heterogeneity in terms of patches, patch size and associated ecotones that is common under natural conditions (Main, 1987 in Roberts, D.C., 1990). It is also likely that patches may themselves move around in space (Usher, 1987 in Roberts, D.C., 1990) and if areas are too small, or are themselves too patchy through anthropogenic disturbance, this may either not be possible, or may be deleterious to the communities concerned.

To understand gap and population dynamics, Martines-Ramos, Alvarez-Buylla and Sarukha'n (1989) state that data are needed on the following:

1. Areas covered by patches of different sizes and ages since disturbance, as well as transition probabilities among patches of different age and size.
2. Probabilities of occurrence of propagules in these different patches.
3. Rates of survival, growth, and reproduction of trees in these different patches.
4. Probabilities that gaps of a given size and age affect trees in one or more life cycle stages.
5. Rates of change in demographic parameters as gaps of given sizes and ages change.

Martinez-Ramos *et al.* state that different species will require studies varying in spatial and temporal scale. In very small forests, this necessity for studying large numbers of trees i.e. over large areas, is likely to be problematic. Neither is anthropogenic disturbance in such small forests necessarily manifested in the form of gaps, rendering the above five research priorities of little value. Indeed the question of how to study non-gap disturbances, such as one finds in urban areas, is one to which ecologists have paid scant attention. Brokaw (1985) states that because of disturbance variation, the importance of community history, the probabilistic nature of dispersal, and the existence of different kinds of competitive hierarchies,

disturbance has been shown to result in unpredictable species composition within gaps, and that this variation may vary for different kinds of trees (Brokaw and Scheiner, 1989). This kind of thinking relates particularly to section 7. on sampling. Connell (1989) suggests that the species composition of trees filling gaps will be in part a consequence of those events and processes that determined the survival of seedlings and saplings during prior years. This thesis contends that this may be equally so in the wide variety of non-gap disturbances encountered in the Durban forests. It is suggested that variously disturbed communities are infinitely more complex than simple dynamic mosaics of vegetation patches. Heterogeneity needs to be characterised at a finer level of resolution, and this renders attempts at description, quantification and sampling more difficult.

Such conjecture clearly emphasizes the role of the observer in defining scale, and suggests there are no easy ways to divide the continuum of environmental fluctuations into normal and disturbance regions (Bazzaz and Sipe, 1987). It is not surprising that generalizations about disturbance across different scales and community types encounter difficulties (Bazzaz and Sipe, 1987), and natural change, whether consisting of varying spatial distributions of trees (Raal, 1990), varying size-class distributions (Muir, 1990b), cyclic replacements or successional trajectories, complicates the testing of hypotheses about human-induced disturbances (Pickett and White, 1987). Disturbance occurs at all ecological levels of organisation, and its effects merge with man-induced changes over various spatial scales and time frames (Pickett and White, 1985). Even a gap, albeit a readily understood notion, is a term which on closer examination reveals considerable imprecision (Swaine, Lieberman and Putz, 1987). A gap is usually defined as an opening in a forest canopy caused by the death of one or more trees (in urban areas gaps may have many origins), which makes available the resources previously used by the missing trees (Lieberman *et al.*, 1987). Light, arguably, is the most relevant resource, but an equivalent gap presumably exists in the rhizosphere (Lieberman *et al.*, 1987). In the literature it is not always clear whether the gaps discussed include or exclude those caused by tree death, which do not cause a break in the upper canopy, and the definition of gaps is often unclear, while their 'size' is difficult to measure. Structural definitions are superficial and awkward to apply (Lieberman *et al.*, 1987). "Biologically, a gap is multidimensional; (as discussed in section 17.6.) incorporating structural, microclimatic, edaphic and biotic changes; and its size (and existence) is not absolute, but is relative to the organism which perceives it" (Lieberman *et al.*, 1987).

The gaps and disturbances within them aside, even individual forests can display sharp local contrasts in both floristic composition and structure over small spatial scales, and these differences can be accentuated by anthropogenic disturbance e.g. the Afromontane forests of the Transkei (Cawe and McKenzie, 1989). Within the Greater Durban area, MacDevette, MacDevette, Gordon and Bartholomew (1989) showed forests representative of

both Mozambique Coastal Plain Forests and Natal Coastal Forests to occur. Under Natal Coastal Forests, the Silverglen Group Forests were found to include Pigeon Valley, Silverglen Nature Reserve and Burman Bush, while under Mozambique Coastal Plain Forests, Southern Coastal Forests were found to include the Hawaan and Peace Cottage Forests.

These features of disturbance have led to two frequent misinterpretations in field ecology (Pickett and White, 1985).

1. Extrapolation of events measured in disturbance-free years to predict future system states.
2. Use of a plot scale that integrates different kinds of patches (i.e. the problem of scale of resolution at which disturbance is characterised, see above).

The views of these authors should be considered in relation to section 7. on sampling.

Preservation of natural systems necessarily involves a paradox in that we seek to preserve systems that change, by trying to understand how community dynamics are affected by the disturbances that are responsible for such change, and indeed, how such change, in the form of disturbance, may be used as a management tool itself. Knowledge regarding what constitutes acceptable levels of disturbance is lacking (Roberts pers.comm.)

Notwithstanding the financial, organisational and logistical difficulties and constraints faced by managers (see Roberts, D.C., 1990) it is hoped the preceding discussion will have suggested the theoretical difficulties of attempting these tasks.

21. New Perspectives for a new science.

"As we drive up the river road,
there are sixty thousand trees
which I see but do not touch.
Like me, Amanda is confined in
the speeding jeep, but she
touches every tree"

entry May 10

Notebook of M.Marvellous

-- from *Another Roadside Attraction* by Tom Robbins --

"The tree is at each instant a new thing;
we assert form because we do not grasp
the subtlety of an absolute movement"

--- Friedrich Nietzsche ---

There is a complex interweaving of spatial scale, temporal scale and fundamental mechanism that attends the understanding of forest ecology (Shugart, 1990). Environmental disturbance regimes, biotic responses, and associated vegetational patterns

need to be viewed in space-time domains in which the scale for each process or pattern reflects the kind of sampling, and the sampling intervals required to observe them (Shugart, 1990). It is little wonder that Pickett and White (1985) consider that variance generated by patch dynamics is likely to be one of the most important constraints on sampling strategies, and one which has seldom been considered in designing or carrying out field sampling projects (such opinion relates specifically to section 7. on sampling).

In small, isolated, highly disturbed forests with constantly changing spatial scales of heterogeneity, in which the 'ghost of disturbance past', although wholly continuous with the present, cannot be known, and in which the averaging aspect of the landscape is lost (Shugart, 1990), the dynamics of the landscape and the presence of patches in the landscape become less predictable. Consequently, the approaches of the past, emphasizing equilibrium, constancy, homogeneity, stability and predictability become less fitting. As this happens, theory too, becomes increasingly contingent, and presupposed. In a world that is spatially mosaic and episodic at all scales (i.e., fractal or rough) (Steele, 1989) it makes sense to move away from the mechanistic cast of mind that has dominated science for two centuries, and to accept nature as infinitely rich, subtle, and irreducible (Peat, 1991). Even in the pure sciences it is probable that even if the basic equations to describe phenomena were known, "the total system would be insoluble in a numerical sense, and, even if it were possible, a computer 'solution' could be 'opaque' conceptually" (Steele, 1989).

Ecology is an endeavour which impels its practitioners away from reductionist, mechanistic modes of thinking. As the branch of science in which relationships are most compelling, it is an especially interconnected one. As such, conceptual advances in thinking in the pure sciences are all developments of which ecologists should be aware.

Sheldrake's Theory of Formative Causation, Bell's Theorem, Prigogine's Theory of Dissipative Structures, Thom's Mathematical Topology and Bohm's implicate order all challenge traditional notions of causality and the mechanistic principles contained therein. They oblige scientists to reconsider their views on self-organisation and maintenance of natural systems in far-from-equilibrium states, the way in which we perceive separate entities and the forces that govern their interactions, and the concept of hierarchically related causes (Holroyd, 1989). Ecology is well placed to make use of developments in Cybernetics, Fuzzy Set, Chaos, Field, Bootstrap and General Systems Theory. Ecology is part of a science in transition and as such, how it is conducted is no less important than the facts it produces (Mentis, 1988a). To ignore this is to ignore the philosophical relevance of scientific method itself, and it is arguable whether a science lacking in overly successful principles or precedents should be prescriptive.

Increasingly, science is discovering that nonlinearity is the norm, whereas truly linear systems are the exception in nature,

or are crude approximations to more subtle nonlinear behaviour (Peat, 1991). Nonlinear systems include those in which what happens in one region depends sensitively on what happens in another (Peat, 1989; Gleick, 1987). General Systems Theory suggests that, in open systems, it is not input that determines outcome, but what happens to the input within the system, or, how it is registered and used in terms of the system's highly structured organisation (Macy, 1991). As Laszlo (in Macy, 1991) affirms, "This is directly contrary to linear causality input-output systems." Such perspectives may be relevant to the study of succession as suggested by Finegan (1984).

Such a view undermines the notion, inherent in the linear concept of causality, that similar conditions produce similar results and that different conditions will produce different results (Macy, 1991). This unquestioned law of causality in classical philosophy and science has guided much research, leading scientists to seek the explanation for differences between phenomena in their initial conditions rather than in ongoing inter- and intrasystemic dynamics (Macy, 1991). Systems can thus produce different results from the same initial inputs or similar results from differing inputs, biology yielding many examples of the latter (Macy, 1991). The relevance of such perspectives (suggestive of the indirect causality of which ecologists are already aware) for the study of gap dynamics is obvious. These perspectives also relate to section 7. on sampling.

Increasingly, these perspectives suggest that Ecological Management is not necessarily something which can be approached through rigid adherence to theory and quantification. As Mentis (1980) states, tested and currently irrefuted hypotheses may be useful provisional explanations of events, but may be overturned, or superseded by better explanations in the future. Thus, not only does scientific knowledge always retain an element of uncertainty, but ecological systems themselves are variable, each one being more or less unique, exacerbating errors in observation and interpretation (Mentis, 1980).

22. Management Recommendations

1. Try to ascertain how well represented species are in all the height classes (or even just the structural classes, if this is all person-power constraints would allow for). This may provide an indication of how episodic recruitment is, giving an idea of the health of the species populations concerned. Such data would have to be interpreted with caution, however (see section 20.3.).
2. Conduct surveys to ascertain whether or not there are species or species groupings occurring only in particular height classes. Restriction to very few height classes may provide an indication of the vulnerability or disturbance impact of the species concerned.
3. Sampling and ordinations should be redone to see if patterns and separations change as one changes the placing of quadrats, thereby sampling different elements of the mosaic in each forest. Describing internal heterogeneity within a forest is important,

as this is a reflection of disturbance, and information on what constitutes healthy levels of disturbance is both crucial, and lacking. In posing questions, it is important to describe the changing spatial disposition, and dynamics of different elements of the forest mosaic, as these elements change through time. This suggests the importance of long-term monitoring.

4. Sequentially increase inclusiveness of ordinations to see if separation changes.

5. Attempt to describe the effects of different canopy types on the forest floor below them e.g. *Trema orientalis* and *Chaetacme aristata* for instance differ widely in the sub-canopy environments that they create. Where these species occur in high numbers, as they often do, this may be of consequence for forest dynamics.

6. Despite the problems concerning their definition, gaps and margins do need to be specifically studied. It needs to be borne in mind however, that edge or margin species are, in the case of Durban, sometimes simply species that have been left on the edges of disturbed habitats, rather than edge specialists themselves.

7. Size structures for woody species should be compared for different quadrats in the same locality. This would give an indication of the mosaic nature of the forest at a different spatial scale, allowing for possible insight into future system states at a scale at which it would be feasible to monitor the accuracy of predictions or expected occurrences, e.g. through the use of permanent quadrats. This could conceivably aid researchers in posing more appropriate questions. By monitoring such forest-specific processes in the long term, and by interpreting data only with reference to the particular forest involved, one may be able to avoid making interpretations in terms of general population dynamic theory which may not hold at the spatial scale of the forest concerned. This does not preclude the identification of trends which may become evident by comparing different forest-specific demographic processes.

8. Some attempt should be made to describe the effect of creepers in the forest canopy on dynamics. Creepers such as *Ipomoea* are potentially problematic, smothering individual trees and areas of the canopy in the more disturbed forests e.g. Burman Bush, Pigeon Valley.

9. Hypotheses should be considered that can be tested at both species and structural levels, for a number of localities, e.g. it is suspected that structural and floristic diversity is lost in Durban forests with decreasing disturbance (Nichols, *pers. comm.*), and this is suggested, both floristically and structurally by certain quadrats in Stainbank, Silverglen and Burman Bush. Integrating structural and floristic considerations in the posing of research questions is important, as the three-dimensional structure of forests determines their internal microclimates and the energy available for other organisms, determining the distribution of biota contained within the forest (Richards, 1983 in Geldenhuys, Knight, Russell and Jarman eds., 1988).

10. Investigate the need to use different sampling approaches in different forests, depending on relative size and degree of disturbance.
11. Try to ascertain whether or not plants are responding primarily to disturbance conditions/gradients and only secondarily, if at all, to environmental gradients.
12. Try to ascertain how static ratios between seedlings, saplings and mature canopy trees are. If the ratios can be accurately monitored over time, this may provide some idea of the difference between recruitment and survival in disturbed areas. Recruitment can be expected to equate more closely with what is in the understorey.
13. A management strategy should be devised that is based on low intensity monitoring, as this study occurred over a limited period of time.
14. More specific attempts should be made to determine whether or not disturbance is manifested mainly structurally or floristically.
15. More specific attempts should be made to distinguish between disturbance, and the patch-structured nature of the forest environment, although these distinctions are largely ones of scale and definition.
16. Investigate ways of using the DBH data that were collected. Analyses of diameter distribution in regression and multivariate studies present many difficulties, e.g. are mathematical fits of diameter distributions biologically meaningful when a high degree of variability of tree numbers within various size classes has been found (Anonymous, 1978 in Geldenhuys et al., 1988) See section 20.3.. DBH data may suggest different things depending on the breakdown of DBH categories into which trees are placed i.e. absolute values are not taken. This fact requires careful consideration when DBH data are analysed.

23.

CONCLUDING REMARKS

Descartes to DECORANA: Is there a better way?

"And we have known biologists who
did proliferate in all directions: one
or two have had a little trouble about it."

-- John Steinbeck in *Log from the Sea of Cortez* --

But our spurned senses reply, "Wretched intellect. You get
your evidence from us, and you try to overthrow us? Your
victory is your defeat."

Democritus

"I believe we will dance together some day. Before then will I
have to have been a trout, bear scars from your stabbing misses
and so have some deeper knowledge? Then will we dance?"

Barry Lopez, *The search for the Heron in Dance of the Herons*.

"One may gain or seek to cultivate a cosmologically based sense of identification in a wide variety of ways...many naturalists and field ecologists, for example, effectively come to experience themselves as leaves on the tree of life and seek to defend the unfolding of the tree in all its aspects as best they can"

Warwick Fox in *Toward a Transpersonal Ecology*.

"Indeed, the particularity of matter, the thingness of things, is helpful to the mind in returning it to the immediacy of experience. For it is not through its fancies....nor the concepts to which it tenaciously clings, that mind is illumined. It is through attention to the here and now, the immediacy of experiencing what eludes its fabrications, that mind can overleap its old self-enclosing constructs and perceive the living process of which it is a part."

Joanna Macy in *World as Lover, World as Self*.

The title of this section refers to the French philosopher René Descartes (1596-1650) who played a leading role in the establishment of scientific method in the seventeenth century. Cartesian thinking is specifically dualist in content in that it holds that the awareness and activity of the subjective mind is separate from what is outside of it i.e. matter, the world, nature or some objective substructure. "While this substructure may be 'knowable by description' in terms of the constructs of mathematical physics, it is not thought to be 'knowable by direct acquaintance'" (Poynton, 1991). Cartesian thinking thus sets in place an intractable dualism, separating mind from matter and people from nature. In contrast, Phenomenology maintains that "all levels of causal substructure are open to direct acquaintance" (Poynton, 1991). Dualism is thus specifically rejected "and the workings of nature are held to be in principle knowable", allowing us to approach the "truth" (Poynton, 1991). The ecophilosopher Neil Evernden writes that "Descartes builds a barrier between man and nature and invites us to guess what is on the other side" (Evernden, 1985). In adopting this world of guesses in preference to our own experience, Descartes is considered to have bequeathed us with a sense of separation and a way of knowing, both of which discourage any sense of identification with and care for nature.

The picture of forests that emerges from this study is one of a complex mosaic of multivariate and highly interactive determinants which are complicated on a variety of scales by historical and ongoing disturbances, many of which have undetectable and poorly quantifiable results at spatial and temporal scales which defy resolution. Indeed, community and ecosystem heterogeneity "can be detected at all spatial scales" (Palmer, 1992). The plants that we study, their own biology apart, are integrators at many scales of inscrutable disturbance histories, and already, after a six-year study, is it being claimed that "prevalent concepts of tolerance and gap dependence for tropical wet forest trees need to be abandoned or greatly refined" to reflect "the complex size-dependent patterns of life history differences and similarities that exist among species" (Clark and Clark, 1992). In the case of Durban forests, six years is too long to wait before new theories can be evaluated, or action taken.

This needs to be borne in mind when evaluating new scientific techniques which have little chance of real life application in what is becoming increasingly a crisis discipline. While theoretically enlightening and overdue, recent approaches linking forest dynamics to fuzzy set (Moraczewski, 1993), chaos (Palmer, 1992) and metapopulation theory (Wu, Vankat & Barlas, 1993; Hastings and Wolin, 1989) by way of sophisticated modelling techniques have little hope of successful application in arenas where management efforts are increasingly dictated by demography, politics, training, available time and personpower and severe financial restrictions (see section 17.8. paragraph 5).

Furthermore, this view of forests underscores General Systems Theory thinking which asserts the "radical interdependence of

phenomena" (Macy, 1991), and is consistent with the idea that "factors of existence are mutually determined, providing occasion and context for each other's emergence and subsiding" (Macy, 1993). According to this idea, "things do not produce each other or make each other happen, as in linear causality; they *help* each other to happen by providing occasion or locus or context, and in so doing, they in turn are affected. There is a mutuality here, a reciprocal dynamic" (Macy, 1993). This gives cause for reflection, for instance, on the uses of multivariate methods which attempt to maximise variation in data sets along specific linear axes. As stated previously "This view undermines the notion, inherent in the linear concept of causality, that similar conditions produce similar results and that different conditions will produce different results. This idea has guided much research, "leading scientists to seek the explanation for differences between phenomena in their initial conditions rather than in their ongoing inter- and intrasystemic dynamics" (Macy, 1991). Macy (1991) states that these dynamics can "produce different results from the same initial inputs or similar results from differing inputs", the latter being, to some degree, characteristic of biological systems (Macy, 1991). Much of the above is implicit in sections 15.1., 19.3., 19.6., 19.7., 21. and 7., and indeed, in much of this thesis, although biologists seldom express themselves in such terms. See the references to causality in section 11.1. and comments on process, pattern and mechanism in section 15.1..

Despite this, biologists have been slow to consider that at some levels of complexity, patchiness, heterogeneity and disturbance, the limitations of formal methods and procedures of sampling, description, interpretation and comparison, especially between unique forest situations, render them of questionable value. This may be largely a result of paradigmatic inertia, (see section 11. point 4.) wherein scientific work is not seen as valid unless it is quantitative, and there is no existing framework for dealing with qualitative data or phenomena that may be important beyond their numerical detectability. Section 11. is generally helpful here in suggesting why this inertia may exist among biologists.

As a result of the above, this work has been directed to suggesting the philosophical coherence of an alternative approach to research in which the scientist is more directly able to "mentally extend or project oneself into the object of study" (Root-Bernstein, 1990), in which "The subject of inquiry ceases to be external", and "the observer identifies with that subject and dwells within it" (Root-Bernstein, 1990) rather than trusting rigid methodologies and the assumptions behind them to make sense of irreducible mental and physical phenomena. Influenced by its own history, and by broader philosophical and cultural history as it is (Poynton, 1991), such research approaches are still unfamiliar to western thinking "which is a long way yet from explicitly integrating the inferring process of science with direct experiential seeing" (Poynton, 1980). As has been stated in section 19.2.1., it is difficult to prescribe exactly how such an approach should be tackled, and Poynton (1985) states that "The subject matter of biology may be

inherently more intractable to substructural investigation than is the subject matter of physics" and admits that "the complexity of biological phenomena has tended to retard the development of fundamental theory and ontology in the biological sciences" (Poynton, 1985). Some of the reasons for this are discussed by Poynton (1985) and will not be reviewed here, but are alluded to in section 15.1..

The question of how to cultivate the qualities of mind and training skills which permit phenomenological research and presuppositionless observation to proceed is a demanding one, in part because speculation in purely discursive vein runs the risk of continuing in the particularising and abstracting mode which phenomenology specifically attempts to counter. In addition, even concerned writers such as Poynton (1985) and Mentis (1988a) have had little to say on the 'how?' of getting complementary paradigms into operation. This clarification of the 'what?' (is the problem), as opposed to the 'how?' (do we solve it) is in part explicable in that it implies an examination of 'being' and 'seeing' too semantically challenging, personal, and even spiritual (see Comfort's characterisation of spirituality in Poynton, 1980) for the conservatism of 'normal' science. The notion nonetheless remains that the traditional "one-level physicalist" (Poynton, 1980) practice of science is increasingly being questioned by scientists, statisticians and philosophers, as this thesis has attempted to indicate. It therefore seems wise to attempt to steer the often uncomprehending flirtation of these scientists with phenomenological thinking (see section 19.2.1.) in a constructive direction, despite the difficulties of "communicating ontologically based identification in words" (Poynton, 1991).

While intelligible criteria by which to define phenomenological research are elusive, and will not be dealt with in a direct philosophical sense in this work, there are some clues and practical principles which merit explication, and of which the development of this thesis thus far hopes to support. In order to provide some context, however, it is necessary to begin with a brief description of the philosophical fundamentals from which these principles are derived. Whiteman (1967) notes that: "the intelligible structure behind any particular observation, (my emphasis) whether it is of an everyday kind or made in some elaborate scientific experiment", is both "operative in and analyzable out of the total experience (subconscious potentialities included)". Whiteman (1967) concludes "that a direct knowability, that is a phenomenological analysis, of selected regions of the inter-subjective constitution of the universe of nature and humanity is in principle possible". Poynton (1985) notes in this respect that the only limitation to such insight is "lack of ability on the part of the observer" (my emphasis).

As stated above, I do not propose to explore in strictly philosophical terms what the precise qualities of phenomenological observation are as this is too complex a task. Nor do I propose to suggest how, if at all, phenomenological and conceptual analysis (see section 19.2.1.) can be directly used to

manage Durban forests. I shall suggest, however, bearing the philosophical background as stated strongly in mind, that the relationship of observation (as it is generally understood) to observation (in the presuppositionless or phenomenological sense) can be usefully explored. The reason for this is that it (the relationship) constitutes a basis for proposing a different approach to biological research in which the importance of observation, even in its conventionally understood sense, is acknowledged. I propose that, without endorsement of the relationship between observation (ordinary sense) and observation (phenomenological sense), little progress can be made in divesting perception of conditioning that may prevent different modes of interpretation and action from arising, or of "integrating analytic and holistic approaches to research" (Poynton, 1980). The necessity for the aforementioned, especially in the disturbed forests with which this thesis is concerned, should by now be clear to readers (but see section 10. paragraph 4). I shall further argue that this kind of approach gives rise to a fundamentally different attitude to scientific work, and that this in itself is worthwhile for conservation and management in a number of important ways, as initially suggested in section 15.2..

My contention is that there is scientific value in knowing a place intimately, through association and observation, and is specifically constructed to provide a philosophical justification by which skilled naturalists (observers) may contribute to creditable scientific research. I have thus purposefully set up a distinction between observation and quantification, in the hope that scientific work will be encouraged to proceed in a manner facilitating such synthesis as will make the distinction less absolute than is currently the case in plant biological research. I will suggest that the level of resolution at which experienced naturalists are able to observe and to question is such, that with training, this observation may bridge the gap between observation in its conventionally understood sense, and observation in a more phenomenological sense. This thesis has attempted to show that such a pursuit is not only defensible in philosophical terms, but may help to generate useful biological knowledge by avoiding the dangers of "theory- or problem-bound research" (Poynton, 1990) which runs the risk of "predetermining the results" of ecological investigation (Poynton, 1991) and which is often inappropriate in Durban forests. Noteworthy here too are the inherent dangers of hypothesis-testing oriented work as suggested in sections 10. paragraph 4 and 19.2.1..

This kind of knowledge cannot be elucidated by statistical procedures and conventional research alone, nor can it necessarily be taught. Its development can however be encouraged, and it is the conditions that foster this encouragement that should be addressed. It is a knowledge borne of practised observation, ongoing association with, and field experience in a particular place. It is a skill accessible to good naturalists first and foremost, in that their interest is primarily in seeing, noting and describing, as opposed to instituting the prescriptive conceptual methodologies and statistical/quantitative approaches of formal science, so many of

which are plagued by problems of applicability, interpretation and error in small highly disturbed forests (see Whiteman's cautionary note in section 19.2.1.).

It is a skill which should not be replaced by conventional research methods which are becoming increasingly abstract, conceptually intricate and difficult to apply. More importantly, it is a skill that leads not only to an alternative way of knowing, but a better way of caring as attested to by increasing numbers of authors e.g. Heidegger, in Poynton (1991), Fox (1990), Evernden (1985).

The art and process of observation implies field knowledge and experience of what is being observed; hence the requirement for biologists to be good naturalists first and foremost. With practice, familiarity borne of long association, committed personal interest and the sense of identification, participation and care that this process fosters, it is reasonable to speculate that this skill may lead to better experiential seeing, and an ability to detect and appreciate pattern, change and trend in forest environments at useful scales in an ongoing fashion. That the practice of seeing lays a necessary groundwork for any specific attempts at seeing (phenomenological sense) is not something one could be entirely sure of in any philosophical sense. If one is specifically attempting to apply the phenomenological method, however, and given the dearth of pointers in the literature, then this at least constitutes a practical and applicable attempt to begin, difficult though the road may be. While there are other aspects of training that may facilitate and enhance such seeing (such as the adoption of various meditative practices) I do not propose to depart entirely from the realms of biology in order to discuss them.

It is necessary to remember that I am advocating a supplementary rather than a competing approach. It is important to support and encourage theoretical inquiry and it is important to encourage the biologist who theorises, comes, measures and then goes (often only getting to know his/her specimens once he/she is in a herbarium). It is equally important, however, to support and encourage the naturalist who stays, watches, participates, identifies with.....and feels.

The encouragement of this capacity to feel and to care, or attitude of "steadfast friendliness" (Fox, 1990), largely unknown in Western scientific endeavour and teaching, is by no means trivial to the topic of urban conservation and management. This personal shift in emphasis naturally gives rise to attempts aimed not just at understanding, but also to an increasing concern with saving in practical terms, i.e. lobbying, fund-raising, challenging value priorities, debating ecophilosophical issues, social and political action aimed at protection etc. It is this practical action, which at present, in the Durban area, is saving the forests; and not the activities of traditional, theorising biologists, well intentioned though they may be (see also section 18.3.). The challenges and motivations required of understanding are different from those required of acting to save and protect. They demand broader based action and involvement,

and are inspired, impelled and sustained by a wholly different sense of identification than that fostered by the abstract personal remoteness of the biology practised by the traditional scientist. Ultimately, this participation fosters an increasingly intimate sense of engagement and belonging which transcends the mere desire to understand. This notion is expressed by Martin Heidegger in his statement: "The world is not what I think, but what I live through", and it is through this process of 'living through' the world that 'care' arises (Heidegger in Poynton, 1990). The ecophilosopher Neil Evernden states that "we are not in an environmental crisis but are the environmental crisis" (Evernden, 1985) and that "Ecology is learning anew to-be-at-home in the region of our concern. This means that human homecoming is a matter of learning how to dwell intimately with that which resists our attempts to control, shape, manipulate and exploit it" (Grange in Evernden, 1985). Thus the sense of deep identification, participation and belonging to the natural world that the proposed approach fosters, becomes critical in effecting a change in biologists at a personal level. Such cosmologically based identification (Fox, 1990), even if achieved in only a tentative or philosophically undeveloped sense, gives rise to an increasingly urgent motivation not only to study forests, but also to preserve and defend them in as integrated a way as possible. While this is informally attested to in both the Ph. D. thesis and ongoing work of Roberts (1990 - 1993), it is seldom explicitly stated, but should be!!

Phenomenology offers a method of direct encounter with the natural world. In allowing us to directly encounter that which we seek to understand, Phenomenological investigation illumines the nature of our true relationship to it. Phenomenology thus seems to direct us to a state of knowing and caring. As scientists we are in need of them both.

It is important, in conclusion, to establish clearly what this thesis has done about the problems raised. Firstly, and perhaps most importantly, it is widely held in ecophilosophy that the problem of 'what to do' must be preceded by considerations of 'how to be' and 'how to perceive' (Whiteman, 1967, 1986; Needleman and Applebaum, 1990; Fox, 1990; Poynton, 1991; Batchelor and Brown, 1992; Naess, 1992; Macy, 1993). The Ecophilosopher, Pepper, states that "what we do about nature and ecology is a function not of what is 'out there', but of how we perceive it, and our perception is a function of our cultural filter and our assumptions in it" (Pepper in Poynton, 1991). What this thesis has attempted to suggest, is the validity of such notions when it comes to routine science, so much of which is accepted at face value as existing beyond the ambit of such questioning. This thesis has directly suggested then, that the appropriateness of our methods, the assumptions underlying them, and the availability of more suitable methods all affect the ability of the practising scientist to see things as they in fact are. In going to some lengths to suggest that scientific theories and methods are in many instances presupposed constructions and representations, and arguably of questionable relevance, this thesis has produced a scientific and philosophical

incursion into an arena in which the conservatism of science is seldom challenged. This in itself, is seen as being an uncommon, and creative contribution to the field.

Secondly, as an exercise in biophilosophy, this thesis has concerned itself with some of the specific skills required of philosophers. If one attempts to raise questions of paradigm and philosophy, then one of these skills is to realise that a problem of some sort exists, and to communicate this problem to others in such a way as not to sound like mere word-spinning (Poynton, pers. comm.). While this thesis has been lengthy, in an attempt to reveal the relevance of epistemology and critical thinking in a diverse number of fields, it is hoped that the reader will have realised from the cumulative impact of the thesis, that a definite problem exists. If this has been achieved, then it is an end in itself as the history of science is replete with resistance to novel ideas.

Thirdly, and in contrast even to most philosophy, this thesis has taken a problem that scientists traditionally approach in a largely quantitative and statistical manner, and used it as a springboard from which to raise topics ranging from modelling and management to psychology, religion and ontology, suggesting that close attention needs to be paid to all of these topics **together** if any real progress is to be made. In this sense, this thesis represents an unusual, inventive, and hopefully profitable contribution to this particular field.

REFERENCES

- Acocks, J.P.H. (1988). *Veld types of South Africa*. Memoirs of the Botanical Survey of South Africa No. 57. 3rd. edn. Pretoria: Botanical Research Institute.
- Andersen, A.N. (1989). How important is seed predation to recruitment in stable populations of long lived perennials. *Oecologia*. 81: 310 - 315.
- Augspurger, C.K. (1984). Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology*. 65(6): 1705 - 1712.
- Augspurger, C.K. & Kelly, C.K. (1984). Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*. 61: 211 - 217.
- Augspurger, C.K. & Franson, S.E. (1988). Input of wind dispersed seeds into light-gaps and forest sites in a Neotropical forest. *Journal of Tropical Ecology*. 4: 239 - 252.
- Batchelor, M. & Brown, K. eds. (1992). *Buddhism and Ecology*. London: Cassell Publishers Limited.
- Bazzaz, F.A. & Sipe, T.W. (1987). Physiological Ecology, Disturbance and Ecosystem Recovery. In Schulze, E.D. & Zwolfe, H. eds. *Potentials and Limitations of Ecosystem Analysis*. Berlin: Springer-Verlag.
- Bond, W.J. (1989). Ecological Biogeography and Forests. In *Biogeography of the Mixed Evergreen Forests of Southern Africa*. Geldenhuys, C.J. ed. Ecosystem Programmes Occasional Report Series No. 45. Pretoria: C.S.I.R.
- Botha. (1988). In Roberts, D.C.; Baker, C. & Berruti, A. (1989). Proposal for the extension of Roosfontein Nature Reserve. The Wildlife Society of Southern Africa.

- Bredenkamp, G.J.; Theron, G.K. & Van Vuuren, D.R.J. (1983). Ecological interpretation of plant communities by classification and ordination of quantitative soil characteristics. *Bothalia*. 14, 3 & 4: 691 - 699.
- Brokaw, N.V.L. (1982). Treefalls: Frequency, Timing, and Consequences. In *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Leigh, E.G.; Rand, A.S. & Windsor, D.M. eds. Washington: Smithsonian Institution Press.
- Brokaw, N.V.L. (1985). Gap-phase regeneration in a tropical forest. *Ecology*. 66(3): 682 - 687.
- Brokaw, N.V.L. (1985). Treefalls, regrowth, and community structure in Tropical Forests. In *The Ecology of Natural Disturbance and Patch Dynamics*. Pickett, S.T.A. & White, P.S. eds. London: Academic Press.
- Brokaw, N.V.L. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*. 75: 9 - 19.
- Brokaw, N.V.L. & Scheiner, S.M. (1989). Species composition in gaps and structure of a tropical forest. *Ecology*. 70(3): 538 - 541.
- Brown, J.H. & Gibson, A.C. (1988). *Biogeography*. Toronto: C.V. Mosby.
- Burgess, R.L. & Sharpe, D.M. (1981). Summary and Conclusions. In Burgess, R.L. & Sharpe, D.M. eds. *Forest Island Dynamics in Man Dominated Landscapes*. Berlin: Springer-Verlag.
- Busing, R.T. (1991). A Spatial Model of Forest Dynamics. *Vegetatio*. 92: 167 - 179.
- Capra, F. (1982). *The Turning Point - Science, Society and the Rising Culture*. London: Flamingo.
- Cawe, S.G. & McKenzie, B. (1989). The afro-montane forests of Transkei, southern Africa. II: A floristic classification. *South African Journal of Botany*. 55(1): 31 - 39.

- Clark, D.A. & Clark, D.B. (1992). Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*. 62 (3): 315 - 344.
- Connell, J.H. Tropical Rain Forests and Coral Reefs as Open Non-Equilibrium Systems.
- Connell, J.H. (1989). Some processes affecting the species composition in forest gaps. *Ecology*. 70(3): 560 - 562.
- Cooper, K.H. (1985). The conservation status of indigenous forests in Transvaal, Natal, and O.F.S., South Africa. *The Wildlife Society of Southern Africa*.
- Cowling, R.M. Introduction. In Cowling, R.M.; Le Maitre, D.C.; McKenzie, B.; Prys-Jones, R.P. & van Wilgen, B.W. eds. (1987). Disturbance and the dynamics of Fynbos biome communities. South African National Scientific Programmes Report No. 135. Pretoria: Council for Scientific and Industrial Research.
- Crawley, M.J. (1990). The population dynamics of plants. *Philosophical Transactions of the Royal Society of London*. 330: 125 - 140.
- Davies, D.H. (1986). When ! - Reform and change in the South African city. *South African Geographical Journal*. Vol. 68 No. 1.
- Deall, G.B. & Theron, G.K. (1990). Ordination as a tool for substantiating and interpreting floristic classifications: a case study. *Bothalia*. 20.2 223 - 227.
- Daimond, J.M. (1982). Implications of island biogeography for ecosystem conservation. In *Conservation of ecosystems: theory and practice*. Siegfried, W.R. & Davies, B.R. (eds.). South African National Scientific Programmes Report No. 61. Pretoria: C.S.I.R.
- Digby, P.G.N. & Kempton, R.A. (1987). *Multivariate Analysis of Ecological Communities*. London: Chapman and Hall.

- Dyer, R.A. (1976). *The Genera of Southern African Flowering Plants*. Vol.2. Gymnosperms and Monocotyledones. Pretoria. Department of Agricultural and Technical services.
- Ehrlich, P.R. & Murphy, D.D. (1987). Monitoring populations on remnants of native vegetation. In *Nature Conservation: the role of remnants of native vegetation*. Saunders, G.W.; Burbidge, A.A. & Hopkins, A.J.M. eds. Chipping Norton, New South Wales: Surrey Beatty.
- Ehrlich, P.R. (1989). Discussion: Ecology and Resource Management - Is Ecological Theory Any Good In Practice. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Eldredge, N. & Gould, S.J. (1972). Punctuated Equilibria: an alternative to phyletic gradualism. In *Models in Palaeobiology*. Schopf, J.J.M. ed. San Francisco: Freeman, Cooper & Co.
- Equihua, M. (1990). Fuzzy clustering of ecological data. *Journal of Ecology*. 78, 519 - 534.
- Evernden, N. (1985). *The natural alien: humankind and the environment*. Toronto: University of Toronto Press.
- Everard, D.A. (1986). The effects of fire on the *Podocarpus latifolius* forests of the Royal Natal National Park, Natal Drakensberg. *South African Journal of Botany*. 52: 60 - 66.
- Finegan, B. (1984). Forest succession. *Nature*. Vol. 312, 109 - 114.
- Foran, B.D.; Bastin, G. & Shaw, K.A. (1986). Range Assessment and Monitoring in Arid Lands: the Use of Classification and Ordination in Range Survey. *Journal of Environmental Management*. 22, 67 - 84.
- Fox, W. (1990). *Toward a Transpersonal Ecology, Developing New Foundations for Environmentalism*. London: Shambhala.
- Gauch, H.G. (1982). *Multivariate analysis in community ecology*. Cambridge: Cambridge University Press.

- Geldenhuys, C.J. ed. (1989). Biogeography of the Mixed Evergreen Forests of Southern Africa. Occasional Report No. 45. Pretoria: Council for Scientific and Industrial Research.
- Geldenhuys, C.J.; Knight, R.S.; Russell, S. & Jarman, M.L. eds. (1988). *Dictionary of Forest Structural Terminology*. South African National Scientific Programmes Report No. 147. Pretoria. C.S.I.R.
- Geldenhuys, C.J. & van Laar, A. (1980). Interrelationships between Vegetation and Site Characteristics in the Gouna Forest. *South African Forestry Journal*. 112, 3 - 9.
- Gigon, A. (1987). An Hierarchic Approach in Causal Ecosystem Analysis. The Calcifuge-Calcicole Problem in Alpine Grasslands. In *Potentials and Limitations of Ecosystem Analysis*. Schulze, E.D. & Zwolfe, H. eds. Berlin: Springer-Verlag.
- Gleick, J. (1988). *Chaos: Making a new science*. London: Cardinal.
- Gleick, J. & Porter, E. (1990). *Nature's Chaos*. London: Scribners.
- Godfray, H.C. & Blythe, S.P. (1990). Complex dynamics in multispecies communities. *Phil. Soc. R. Soc. Lond.* 330: 221 - 233.
- Goldstein, R.A. & Grigal, D.F. (1986). Analysis of Ecosystem Dynamics and structure, using Numerical Classification and Ordination. In *Ecosystem Theory and Application*. Polunin, N. ed. John Wiley & Sons Ltd.
- Goodall, D.W. (1977). Dynamic Changes in Ecosystems and their Study: The Roles of Induction and Deduction. *Journal of Environmental Management*. 5: 309 - 317.
- Green, R.H. (1984). Statistical and nonstatistical considerations for environmental monitoring studies. *Environmental Monitoring and Assessment*. 4: 293 - 301.

- Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*. 52(4): 107 - 145.
- Halpern, C.B. (1988). Early successional pathways and the resistance and resilience of forest communities. *Ecology*. 69 (6): 1703 - 1715.
- Harper, J.C. (1977). *Population Biology of Plants*. London: Academic Press.
- Harper, J.L. & White, J. (1974). The Demography of Plants. *Annual Review of Ecology and Systematics*. 5: 419-463.
- Harrison, E.A. & Shugart, H.H. (1990). Evaluating performance of an Appalachian oak forest dynamics model. *Vegetatio*. 86: 1 - 13.
- Hartshorn, G.S. (1989). Gap-Phase dynamics and tropical tree species richness In *Tropical Forests: Botanical Dynamics, Speciation and Diversity*. Holm-Nielsen, I.C. & Balslev, H. eds. New York: Academic Press.
- Hastings, A. & Wolin, C.L. (1989). Within-Patch Dynamics in a Metapopulation. *Ecology*. 70, 5: 1261 - 1266.
- Hill, M.D. (1979). DECORANA - A FORTRAN programme for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, New York.
- Hill, M.O. & Gauch, H.G. (1980). Detrended Correspondence Analysis: An improved ordination technique. *Vegetatio*. 42: 47 - 58.
- Hinds, W. (1987). Towards Monitoring of Long-Term Trends in Terrestrial Ecosystems. *Environmental Conservation*. 11 (1): 11 - 18.
- Hobbs, E. (1988). Using Ordination to Analyse the Composition and Structure of Urban Forest Islands. *Forest Ecology and Management*. 23: 139 - 158.
- Holling, C.S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*. 4: 1 - 24.

- Holling, C.S. ed. (1978). *Adaptive Environmental Assessment and Management*. Chichester: Wiley and Sons.
- Holroyd, S. (1989). *The Arkana dictionary of new perspectives*. Suffolk: Arkana.
- Horn, H.S. (1974). The ecology of secondary succession. *Annual Review of Ecology and Systematics*. 5: 25 - 37.
- Horn, S.H., Shugart, H.H. & Urban, D.L. (1989). Simulators as Models of Forest Dynamics. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Hubbell, S.P. & Foster, R.B. Biology, Chance, and History and the Structure of Tropical Rain Forest Tree Communities. In Diamond, J. & Case, T.J. eds. (1986). *Community Ecology*. New York: Harper and Row.
- Hubbell, S.P.; Condit, R. & Foster, R.B. (1990). Presence and absence of density dependence in a Neotropical tree community. *Philosophical Transactions of the Royal Society of London*. 330: 269 - 281.
- Huntley, B.; Siegfried, R. & Sunter, C. (1989). *South African environments into the 21st century*. Cape Town: Human and Rousseau.
- James, F.C. & McCulloch, C.E. (1990). Multivariate analysis in ecology and systematics: Panacea or Pandora's box? *Annual Review of Ecology and Systematics*. 21: 129 - 166.
- Kareiva, P. (1989). Renewing the Dialogue between Theory and Experiments in Population Ecology. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Karr, J.A. (1987). Biological Monitoring and Environmental Assessment: a Conceptual Framework. *Environmental Management*. 11 (2): 249 - 256.
- Kelly, J.R. & Harwell, M.A. (1990). Indicators of Ecosystem Recovery. *Environmental Management*. 14 (5): 527 - 545.
- Kershaw, K.A. (1973). *Quantitative and Dynamic Plant Ecology*. London: Edward Arnold.

- Koehl, M.A.R. (1989). Discussion: From Individuals to Populations. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Levin, S.A. (1989). Challenges in the Development of a Theory of Community and Ecosystem Structure and Function. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Lieberman, M.; Lieberman, D. & Peralta, R. (1989). Forests are not just Swiss cheese: Canopy stereogeometry of non-gaps in tropical forests. *Ecology*. 70(3): 550 - 552.
- Lloyd, J.W. (1989). Discriminant analysis and ordination of vegetation and soils on the Vaalputs radioactive waste disposal site, Bushmanland, South Africa. *South African Journal of Botany*. 55(1): 127 - 136.
- Lubke, R.A.; Morris, J.W.; Theron, G.K. & Van Rooyen, N. (1983). Diversity, structure and pattern in Nyalsvlei vegetation. *South African Journal of Botany*. 2: 26 - 41.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press: Princeton.
- MacDevette, D.R.; MacDevette, D.K.; Gordon, I.G. & Bartholomew, R.L.C. (1989). Floristics of Natal Indigenous Forests. In *Biogeography of the Mixed Evergreen Forests of Southern Africa*. Geldenhuys, C.J. ed. Ecosystem Programmes Occasional Report Series No. 45. Pretoria: C.S.I.R.
- Macy, J. (1991). *Mutual Causality in Buddhism and General Systems Theory*. Albany: State University of New York Press.
- Macy, J. (1993). *World as Lover, World as Self*. London: Rider.
- Margalef, R. (1974). Diversity, stability and maturity in natural ecosystems. In van Dobben, W.H. & Lowe-McConnell R.H. eds. *Unifying Concepts in Ecology*. Report of the plenary sessions of the First international congress of ecology, The Hague, the Netherlands, September 8 - 14, 1974. The Hague: Dr. W. Junk B.V. Publishers.

- Martinez-Ramos, M.; Alvarez-Buylla, E. & Sarukh'han, J. (1989). Tree demography and gap dynamics in a tropical rain forest. *Ecology*. 70(3): 555 - 558.
- Matson, P.A. & Carpenter, S.R. (1990). Introduction to: Statistical Analysis of Ecological Response to Large-Scale Perturbations. *Ecology*. 71 (6): 2037.
- May, R.M. (1976). *Theoretical Ecology: Principles and Applications*. Blackwell Scientific Publications.
- McDonnell, M.J. & Pickett, S.T.A. (1990). Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*. 71 (4): 1232 - 1237.
- Mentis, M.T. (1980). Towards a Scientific Management of Terrestrial Ecosystems. *South African Journal of Science*. 76: 536 - 540.
- Mentis, M.T. (1988a). Hypothetico-deductive and inductive approaches in ecology. *Functional Ecology*. 2: 5 - 14.
- Mentis, M.T. (1988b). Paradigm shifts in South African range science, management and administration. *South African Journal of Science*. 85: 684 - 687.
- Mentis, M.T. & Bailey, A.W. (1990). Changing perceptions of fire management in savanna parks. *Journal of the Grassland Society of Southern Africa*. 7: 2.
- Miller, K.R. Maintaining Ecosystems in Designated Areas. In Siegfried, W.R. & Davies, B.R. (1982). *Conservation of Ecosystems: Theory and Practice*. National Scientific Programmes Report No. 61. Pretoria: C.S.I.R.
- Moll, E.J. (1986). *The Vegetation of the Three Rivers region, Natal*. Natal Town and Regional Planning Report Vol. 33. Pietermaritzburg: Natal Town and Regional Planning Commission.
- Moll, E.J. (1980). A quantitative ecological study of the Hlogwene forest, Natal. *South African Forestry Journal*. No. 114.

- Moll, E.J. & Woods, D.B. (1971). The rate of forest tree growth and a forest ordination at Xumeni, Natal. *Bothalia*. 10, 3: 451 - 460.
- Moraczewski, I.R. (1993). Fuzzy Logic for Phytosociology. *Vegetatio*. 106, 1: 1 -11.
- Muir, D.P. (1990a). Indigenous Forest Utilisation in Kwazulu: A Case Study of Hlatikulu Forest Reserve, Maputaland. Unpublished M.Sc. Thesis. Institute of Natural Resources, University of Natal, Pietermaritzburg.
- Muir, D.P. (1990b). Size Class Distributions. In *Forest Demography and Dynamics*. van Daalen, J.C. ed. Ecosystem Programmes Occasional Report Series No. 48. Pretoria: C.S.I.R.
- Munro, D.D. (1973). Forest Growth Models - A Prognosis. In *Growth models for tree and stand simulation*. Fries, J. ed. International Union for Forest Research.
- Myers, A. & Giller, P.S. eds. (1988). *Analytical Biogeography: An integrated approach to the study of animal and plant distributions*. London: Chapman Hall.
- Naess, A. (1992). *Ecology, community and lifestyle*. Cambridge: Cambridge University Press.
- Needleman, J. & Applebaum, D. (1990). *Real Philosophy: An anthology of the universal search for meaning*. London: Arkana.
- Noble, I.R. & Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*. 43: 5 - 21.
- O'Neill, R.V. (1989). Perspectives in Hierarchy and Scale. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Orians, G.H. (1975). Diversity, stability and maturity in natural ecosystems. In *Unifying Concepts in Ecology*. Report of the plenary sessions of the First international congress of ecology, The Hague, the Netherlands, September 8 - 14, 1974. van Dobben, W.H. & Lowe-McConnell eds. The Hague: Dr W Junk B.V. Publishers.

- Pacala, S.W. (1989). Plant Population Dynamic Theory. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Page, B.R. (1990). Some ideas on management and monitoring in the Northern Tuli Conservation Area, Botswana. Unpublished Report compiled for landholders in the Northern Tuli Conservation Area, Botswana. Durban: University of Natal.
- Palmer, M.W. (1992). The Coexistence of Species in Fractal Landscapes. *The American Naturalist*. 139, 2: 375 - 397.
- Peat, F.D. (1991). *The Philosopher's Stone - Chaos, Synchronicity, and the Hidden Order of the World*. London: Bantam Books.
- Petratis, P.S.; Latham, R.E. & Niesenbaum, R.A. (1989). The Maintenance of Species Diversity by Disturbance. *The Quarterly Review of Biology*. 64 (4).
- Pickett, S.T.A. (1983). Differential adaptation of tropical tree species to canopy gaps and its role in community dynamics. *Tropical Ecology*. 24(1): 68 - 84.
- Pickett, S.T.A. & Thompson, J.N. (1978). Patch dynamics and the design of nature reserves. *Biological Conservation*. 13: 27 -37.
- Pickett, S.T.A. & White, T.S. eds. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. London: Academic Press.
- Pickett, S.T.A. & White, T.S. (1985). Natural Disturbance and Patch Dynamics: An Introduction. In *The Ecology of Natural Disturbance and Patch Dynamics*. Pickett, S.T.A. & White, T.S. eds. London: Academic Press.
- Pickett, S.T.A. & White, T.S. (1985). Patch Dynamics: A Synthesis. In *The Ecology of Natural Disturbance and Patch Dynamics*. Pickett, S.T.A. & White, T.S. eds. London: Academic Press.

- Pickett, S.T.A.; Kolasa, J.; Armesto, J.J. & Collins, S.L. (1989). The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*. 54: 129 - 136.
- Pielou, E.C. (1984). *The interpretation of ecological data, a primer on classification and ordination*. New York: John Wiley and Sons.
- Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*. 307: 321 - 327.
- Platt, W.J. & Strong, D.R. eds. (1989). Introduction to special feature on gaps in forest ecology. *Ecology*. 70(3).
- Pomeroy, M.R.; Hargrove, E.C. & Alberts, J.J. (1987). The Ecosystem Perspective. In Pomeroy, M.R. & Alberts, J.J. eds. *Concepts of Ecosystem Ecology: A Comparative View*. New York: Springer-Verlag.
- Popma, J. & Bongers, F. (1988). The effect of canopy gaps on growth and morphology of rain forest species. *Oecologia*. 75: 625 - 632.
- Poynton, J.C. (1980). Alex Comfort on self and religion. A case study in mergence of Eastern and Western thinking. *Theoria*. Vol. LIV: 1 - 12.
- Poynton, J.C. (1985a). *Hyperolius argus* (Anura) in Natal: taxonomy, biogeography and conservation. *South African Journal of Zoology* 21: 149 - 152.
- Poynton, J.C. (1985b). Ontological frameworks and intelligibility in science. *South African Journal of Philosophy*. 4: 132 - 136.
- Poynton, J.C. (1986). Historical Biogeography: theme and South African variations. *Palaeoecology of Africa*. 17: 139 - 153.
- Poynton, J.C. (1990). Unpublished report to the Natal Parks Board.
- Poynton, J.C. (1991). *Scientific Thinking*. Biology Department, Durban: University of Natal.

- Poynton, J.C. & Roberts, D.C. (1985a). Urban open space planning in South Africa: A biogeographical perspective. *South African Journal of Science*. 81: 33 - 37.
- Preston-Whyte, R.A. (1980). *Climate of Durban*. Pietermaritzburg: Town and Regional Planning Commission.
- Raal, P. (1990). Spatial Distribution of Trees. In *Forest Demography and Dynamics*. van Daalen, J.C. ed. Ecosystem Programmes Occasional Report Series No. 48. Pretoria: C.S.I.R.
- Ray, G.C. Obstacles to the Conservation of Ecosystems. In Siegfried, W.R. & Davies, B.R. eds. (1982). *Conservation of Ecosystems: Theory and Practice*. South African National Scientific Programmes Report No. 61. Pretoria: C.S.I.R.
- Regier, H.A. & Cowell, E.B. (1972). Applications of Ecosystem Theory, Succession, Diversity, Stability, Stress and Conservation. *Biological Conservation*. 4(2): 83 - 88.
- Ridsdill-Smith, T.J. (1987). Measuring and Monitoring Dynamics of Remnants. Types of Organisms that should be Monitored: Why and How. In *Nature Conservation: the role of remnants of Native Vegetation*. Saunders, D.A.; Arnold, G.W.; Burbidge, A.A. & Hopkins, A.J.M. eds. Chipping Norton, New South Wales: Surrey Beatty.
- Roberts, D.C. (1990). An Open Space Survey of Municipal Durban. Ph.D. Thesis. University of Natal, Durban.
- Roberts, D.C. & Poynton, J.C. (1985b). Central peripheral open spaces: need for biological evaluation. *South African Journal of Science*. 81: 464 - 466.
- Roberts, D.W. (1987). A dynamical systems perspective on vegetation theory. *Vegetatio*. 69: 27 - 33.
- Root-Bernstein, R.S. (1991). Discovering the Art in Science. *Dialogue*. 2: 44 - 47.
- Roughgarden, J., May, R. & Levin, S.A. (1989). Introduction. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.

- Rutherford, M.C. & Westfall, R.H. (1986). Biomes of southern Africa - an objective categorisation. *Memoirs of the Botanical Survey of South Africa*. No. 54.
- Rykiel, E.J. (1985). Towards a definition of ecological disturbance. *Australian Journal of Ecology*. 10: 361 - 365.
- Sattler, R. (1986). *Biophilosophy, Analytic and Holistic Perspectives*. Berlin: Springer-Verlag.
- Saunders, D.A.; Arnold, G.W.; Burbidge, A.A. & Hopkins, A.J.M. (1987). The role of remnants of native vegetation in nature conservation: future directions. In *Nature conservation: the role of remnants of native vegetation*. Saunders, D.A.; Arnold, G.W.; Burbidge, A.A. & Hopkins, A.J.M. eds. Chipping Norton, New South Wales: Surrey Beatty.
- Schupp, E.W. (1988). Seed and early seedling predation in the forest understorey and in treefall gaps. *Oikos*. 51: 71 - 78.
- Schupp, E.W.; Howe, H.F.; Augspurger, C.K. & Levy, D.J. (1989). Arrival and survival in tropical treefall gaps. *Ecology*. 70(3): 562 - 564.
- Shackleton, C.M.; Granger, J.E.; McKenzie, B. & Mentis, M.T. (1991). Multivariate analysis of coastal grasslands at Mkambati Game Reserve, north-eastern Pondoland, Transkei. *Bothalia*. 21.1 91 - 107.
- Sheldrake, R. (1990). *The Rebirth of Nature - The Greening of Science and God*. London: Century.
- Shugart, H.H. (1990). Patterns and Ecology of Forests. In *Biogeography and Ecology of Forest Bird Communities*. Keast, A. ed. Ch. 2, The Hague: SPB Academic Publishing b.v.
- Shugart, H.H. & West, D.C. (1980). Forest Succession Models. *Bioscience*. 30 (5): 308 - 313.
- Simberloff, D.S. & Abele, L.G. (1982). Refuge design and island biogeographic theory: effects of fragmentation. *American Naturalist*. 120: 41 - 50.

- Simberloff, D. (1988). The Contribution of Population and Community Biology to Conservation Science. *Annual Review of Ecology and Systematics*. 19: 473 - 511.
- Sloan, A.W. (1967). The nature of science. *Transactions of the Royal Society of South Africa*. 44: 1 - 14.
- Sloan Denslow, J. (1987). Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics*. 18: 431 - 451.
- Sloan Denslow, J. (1980). Gap Partitioning among Tropical Rainforest Trees. *Tropical Succession*. 47 - 55.
- Soule, M.E. (1985). What is Conservation Biology ? *Bioscience*. 35 (11): 727 - 733.
- Soule, M.E. and Kohm, K.A. (1989). *Research Priorities for Conservation Biology*. Washington: Island Press.
- Soule, M.E. & Wilcox, B.A. Conservation Biology: Its Scope and Challenge. In Soule, M.E. & Wilcox, B.E. eds. (1980). *Conservation biology: an evolutionary-ecological perspective*. Sunderland: Sinauer Associates.
- Starfield, A.M. & Bleloch, A.L. (1983). Expert Systems: An Approach to Problems in Ecological Management that are Difficult to Quantify. *Journal of Environmental Management*. 16, 261 - 268.
- Steele, J.H. (1989). Discussion: Scale and Coupling in Ecological Systems. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Steinbeck, J. (1958). *The Log From the Sea of Cortez*. London: Pan.
- Swaine, M.D.; Lieberman, D. & Putz, E. (1987). The dynamics of tree populations in tropical forest: a review. *Journal of Tropical Ecology*. 3: 359 - 366.
- Ter Braak, C.J.F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*. 67 (5): 1167 - 1179.

- Ter Braak, C.J.F. (1987). The analysis of vegetation environment relationships by canonical correspondence analysis. *Vegetatio*. 69: 69 -77.
- Tilman, D. (1989). Discussion: Population Dynamics and Species Interactions. In Roughgarden, J., May, R. & Levin, S.A. eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press.
- Tinley, K.L. (1987). Achieving a Balance Between Long and Short Term Research. In *Nature conservation: the role of remnants of native vegetation*. Saunders, D.A.; Arnold, G.W.; Burbidge, A.A. & Hopkins, A.J.M. eds. Chipping Norton, New South Wales: Surrey Beatty.
- Urban, D.L.; O'Neill, R.V. & Shugart, H.H. (1987). Landscape Ecology: A hierarchical perspective can help scientists understand spatial patterns. *Bioscience*. 37 (2): 119 - 127.
- Van Daalen, J.C.(ed.) (1990). Forest Demography and Dynamics. Foundation for Research Development Occasional Report No. 48. Pretoria: C.S.I.R.
- Van Daalen, J.C. & Geldenhuys, C.J. (1988). Southern African Forests. In Macdonald, I.A.W. & Crawford, R.J.M. eds. *Long-term data series relating to southern Africa's renewable natural resources*. South African National Scientific Programmes Report No. 157. Pretoria: C.S.I.R.
- van Laar, A. & Geldenhuys, C.J. (1975). Distribution and Correlation Patterns in an indigenous Forest. *South African Forestry Journal*. 94, 20 - 28.
- Van Laar, A. & Lewark, S. (1973). Sampling for forest inventories in the indigenous forests of the southern Cape province. *Forestry in South Africa*. No. 14.
- Ward, C.J. (1980). *The plant ecology of the Isipingo beach area, Natal, South Africa*. Memoirs of the Botanical Survey of South Africa No. 45. Pretoria: Botanical Research Institute.
- Weber, R. (1986). *Dialogues with Scientists and Sages - The Search for Unity*. London: Arkana.

- Welden, C.W.; Hewett, S.W.; Hubbell, S.P. & Foster, R.B. (1991). Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*. 72(1): 35 - 50.
- Werger, M.J.A. (1972). Species-area relationship and plot size: with some examples from South African vegetation. *Bothalia*. 10,4: 583 - 594.
- White, F. & Moll, E.J. (1978). The Indian Ocean Coastal Belt. In *Biogeography and ecology of Southern Africa*. Werger, M.J.A. (ed.). The Hague: Dr. W. Junk bv Publishers.
- Whiteman, J.H.M. (1986). *Old and new evidence on the meaning of life, the mystical world view and inner conquest*. Volume 1, an introduction to scientific mysticism. Buckinghamshire: Colin Smythe Ltd.
- Whiteman, J.H.M. (1967). *Philosophy of space and time and the inner constitution of nature: a phenomenological study*. London: George Allen and Unwin.
- Whitmore, T.C. (1988). The influence of tree population dynamics on forest species composition. In *Plant Population Ecology*. Davy, A.J.; Hutchings, M.J. & Watkinson, A.R. eds. London: Blackwell Scientific Publications.
- Whittaker, R.H.; Morris, J.W. & Goodman, D. (1984). Pattern analysis in Savanna woodlands at Nylsvley, South Africa. *Memoirs of the Botanical Survey of South Africa No. 49*. Botanical Research Institute.
- Whittaker, R.H. (1974). The design and stability of plant communities. In van Dobben, W.H. & Lowe-McConnell, R.H. eds. *Unifying Concepts in Ecology*: Report of the plenary sessions of the first international congress of Ecology, The Hague, the Netherlands, September 1974. The Hague: Dr. W. Junk B.V. Publishers.
- Williams-Linera, G. (1990). Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology*. 78, 356 - 373.
- Wolda, H. (1989). The equilibrium concept and density dependence tests : What does it all mean ? *Oecologia*. 81: 430 - 432.

Wolf, F.A. (1984). *Mind .. and the New Physics*. London: Heinemann.

Wu, J.G.; Vankat, J.L.; and Barlas, Y. (1993). Effects of Patch Connectivity and arrangement on animal metapopulation dynamics - A Simulation Study. *Ecological Modelling*. 65: 3 - 4.

Yanitsky, O. Integration of Social and Natural Sciences for Urban Planning. In *Ecology in Practice. Part II: the social response*. (1984). di Castri, F.; Baker, F.W.G.; & Hadley, M. eds. Dublin: Tycooly.

APPENDIX 1: THREE DIMENSIONAL ORDINATIONS OF DURBAN FOREST SITES.

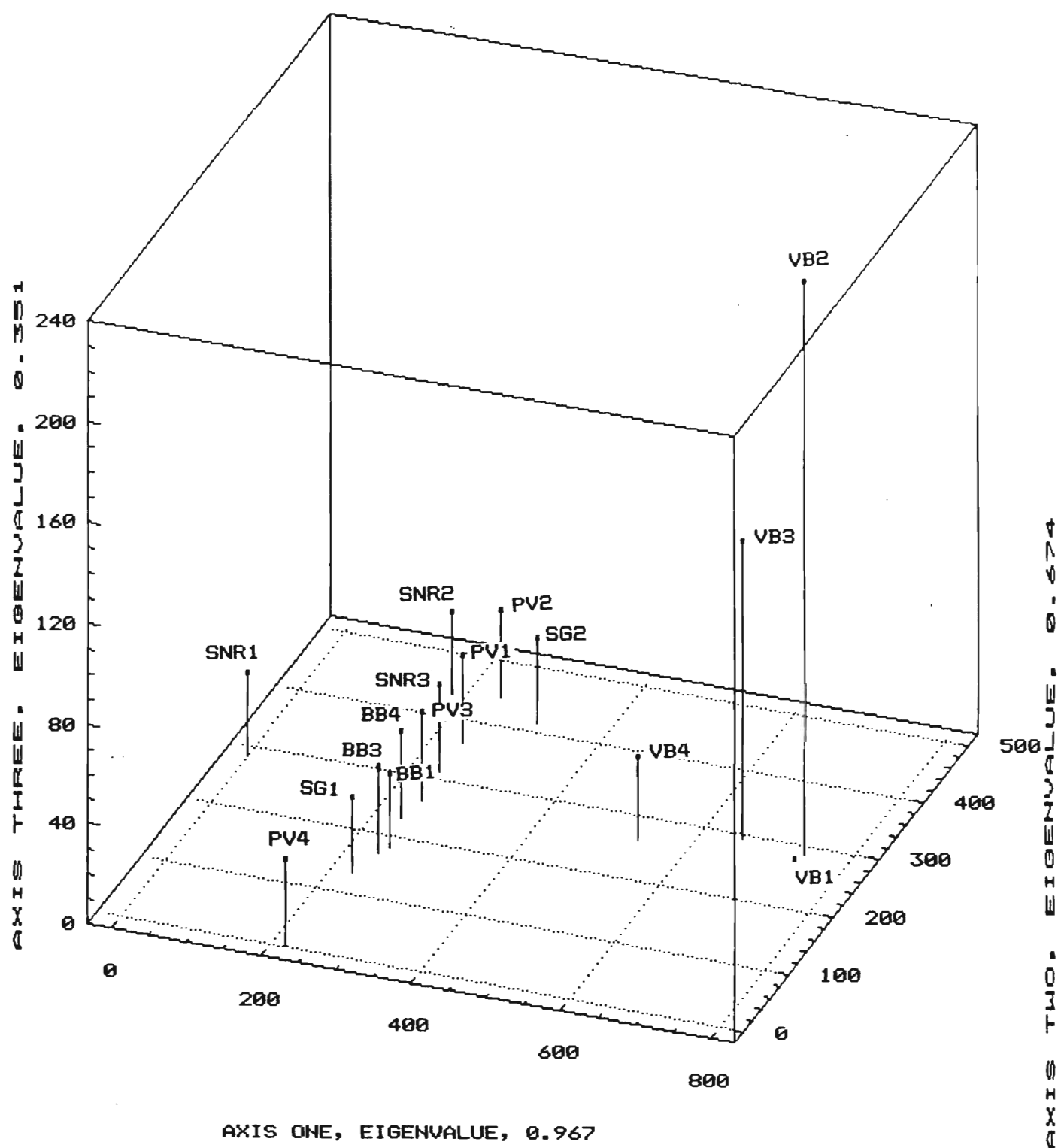


Figure 13 : Three dimensional ordination of seedling species for Durban forest sites.

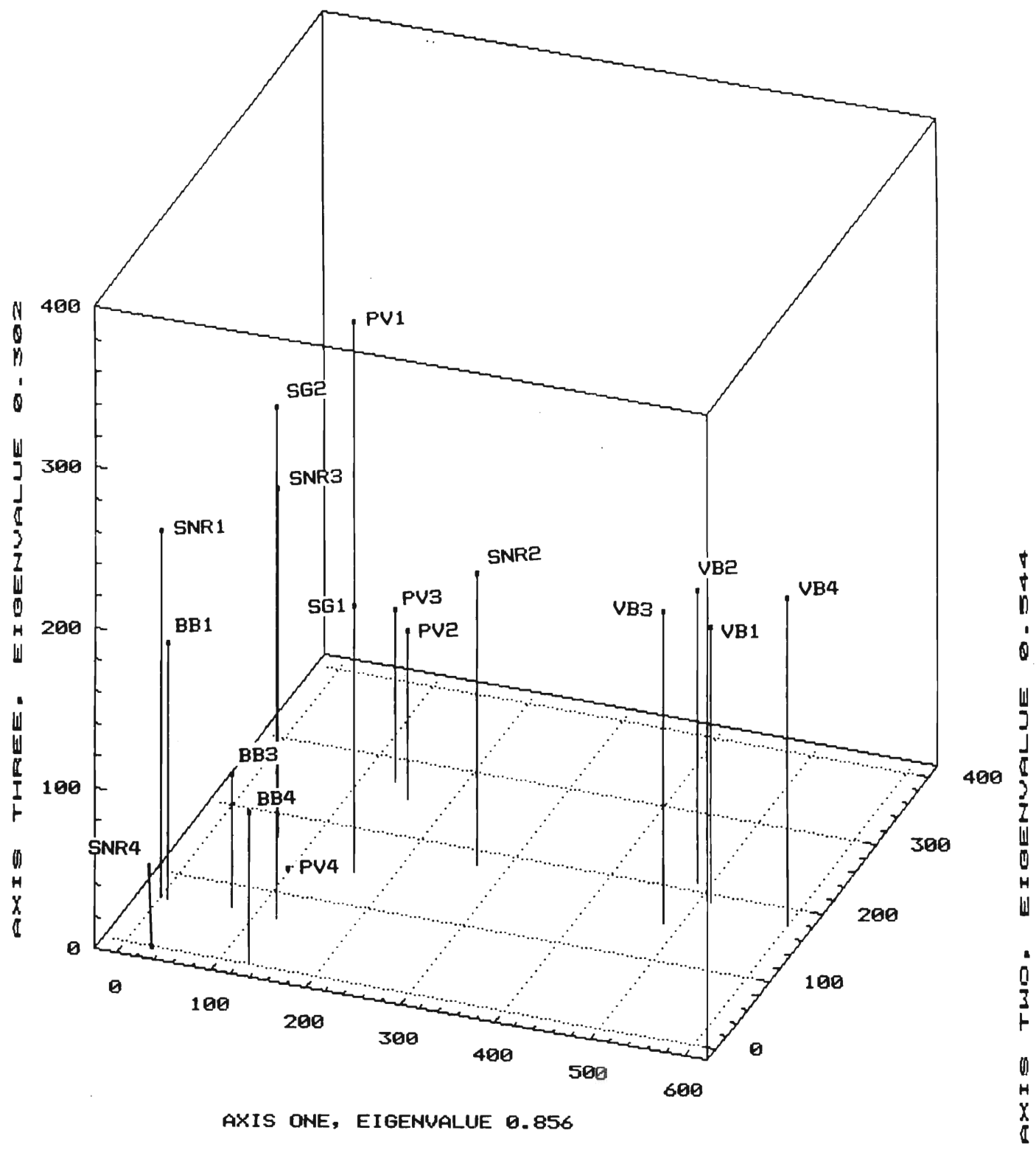


Figure 14 : Three dimensional ordination of sapling species for Durban forest sites.

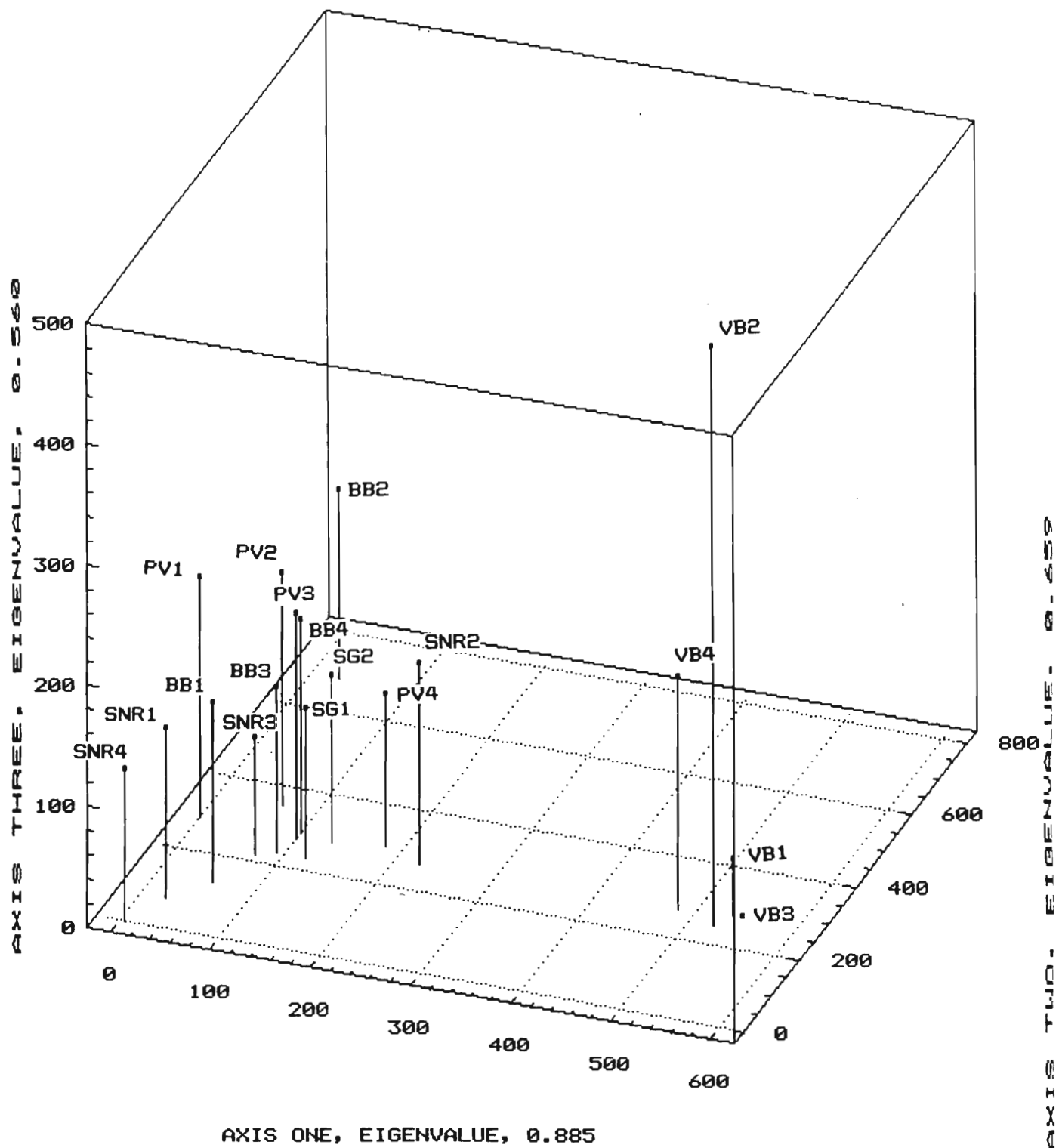


Figure 15 : Three dimensional ordination of understorey species for Durban forest sites.

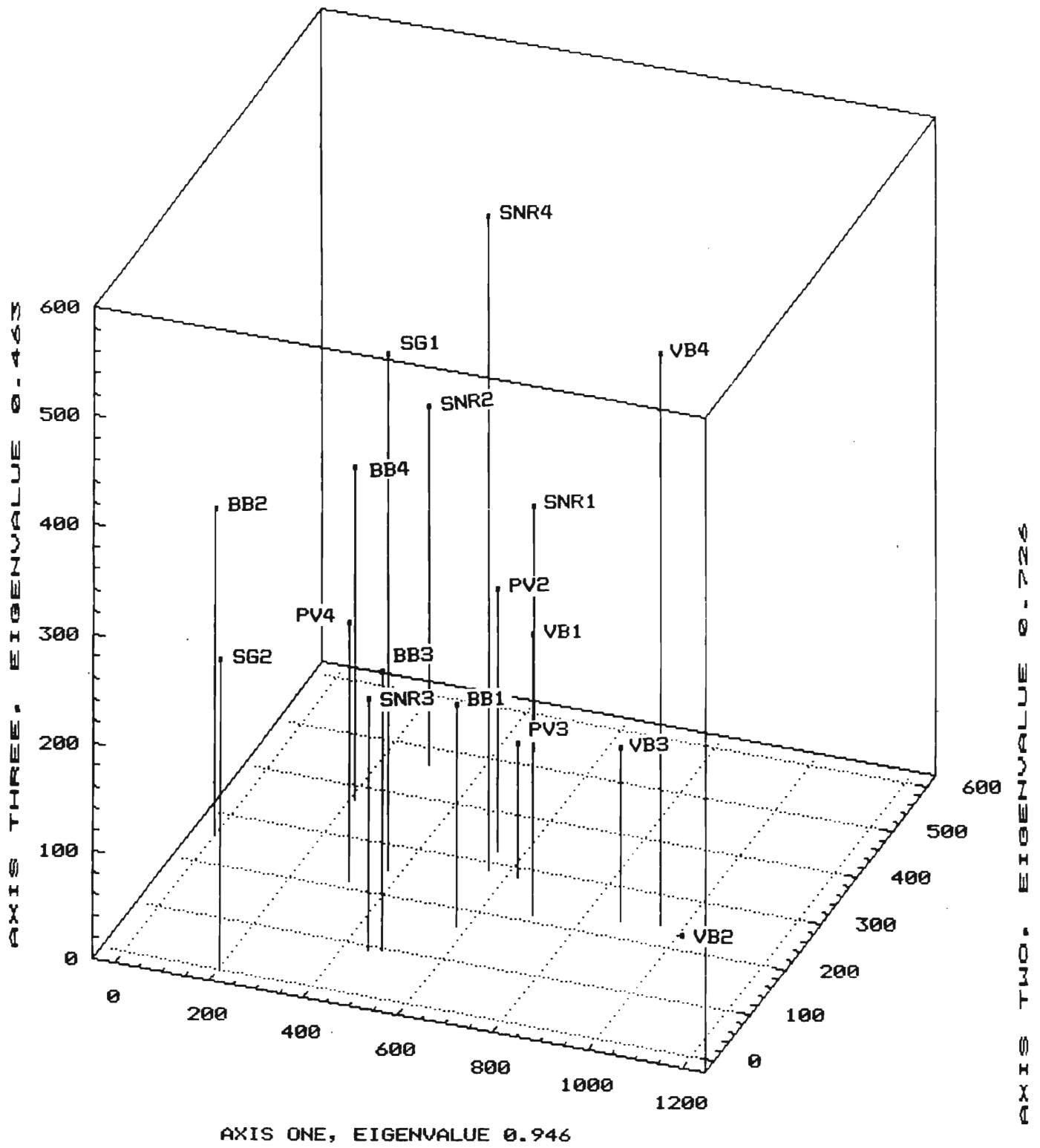


Figure 16 : Three dimensional ordination of canopy species for Durban forest sites.